

New bryozoans from the Upper Ordovician of Morocco and their place in the temperate-to-cool water Mediterranean Province

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A new study of the Upper Ordovician bryozoans belonging to the families Aisenvergiidae, Amplexoporidae, Arthrostylidae, Enalloporidae, Halloporidae, Heterotrypidae, Mesotrypidae, Ptilodictyidae, Rhinidictyidae and Trematoporidae from the eastern Anti-Atlas of Morocco is presented here. These bryozoans come from the calcarenitic levels of the Khabt-el-Hajar Formation, upper Katian, where for the first time the orders Fenestrata and Cryptostomata are described in this formation. This fauna inhabited an upper offshore environment and represent high-energy deposits, typical of a shore face environment, as well as storm-induced deposits. A total of 15 species included in 13 genera, 10 of them only identified in the calcarenitic levels of the Khabt-el-Hajar Formation, and two *incertae sedis* taxa are described. A new species, *Trematopora vesiculata*, is defined. An update of the Upper Ordovician bryozoan presence/absence database, including the 22 genera described in total in the Khabt-el-Hajar Formation, has been carried out. The augmented database has been analysed with two multivariate statistical techniques: detrended correspondence analysis (DCA) and principal coordinate analysis (PCO), in order to assess the palaeogeographic affinity of this fauna, and the results show that Moroccan bryozoans, in spite of belonging to the fauna developed in the highest latitudes during the upper Katian, have a clear Mediterranean affinity. • Key words: Bryozoa, Ordovician, late Katian, Anti-Atlas, Morocco, high and middle-high latitude, Mediterranean region.

JIMÉNEZ-SÁNCHEZ, A., ERNST, A., VENNIN, E. & VILLAS, E. 2016. New bryozoans from the Upper Ordovician of Morocco and their place in the temperate-to-cool water Mediterranean Province. *Bulletin of Geosciences* 91(1), 23–50 (9 figures, 17 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 11, 2015; accepted in revised form October 7, 2015; published online December 4, 2015; issued March 17, 2016.

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During the whole Ordovician the North African Gondwana platforms were mostly dominated by siliciclastic sedimentation, even during the late Katian when carbonate deposits became widely spread on the rest of the Mediterranean platforms. While those carbonate platforms of Iberia, Armorica, Pyrenees, Montagne Noire, Sardinia, Carnic Alps and Tripolitania (Libya) were extensively colonized by a diverse group of invertebrates (Vennin *et al.* 1998), the benthic associations on siliciclastic substrates of the Anti-Atlas region never reached diversity peaks significantly higher than in previous Ordovician times. For instance, the rich *Nicolella* brachiopod fauna (Havlíček 1971, Pickerill & Brenchley 1979), so typical of late Katian times in the south-western European platforms, never colonised the North African region. Nevertheless, bryozoan associations represent locally one exception to the low diver-

sity of the late Katian invertebrate assemblages in North Africa. Carbonate buildups dominated by echinoderm and bryozoan associations have been reported in Libya (Buttler & Massa 1996, Buttler *et al.* 2007) and bryozoan thickets flourished locally on carbonate substrates present in distal parts of some Moroccan platforms during major flooding episodes (Álvaro *et al.* 2007). However, it is one area in the whole of North Africa, close to Erfoud in the eastern Anti-Atlas, which displays an extraordinary bryozoan diversity. The on-going studies on bryozoan associations of the late Katian Khabt-el-Hajar Formation have shown a diversity that parallels those of the Iberian Chains (Jiménez-Sánchez 2009, 2010; Jiménez-Sánchez *et al.* 2010) and the Sardinian occurrences (Conti 1990), and it is only surpassed in the Mediterranean Province by the occurrences studied in the Montagne Noire (Ernst & Key 2007).

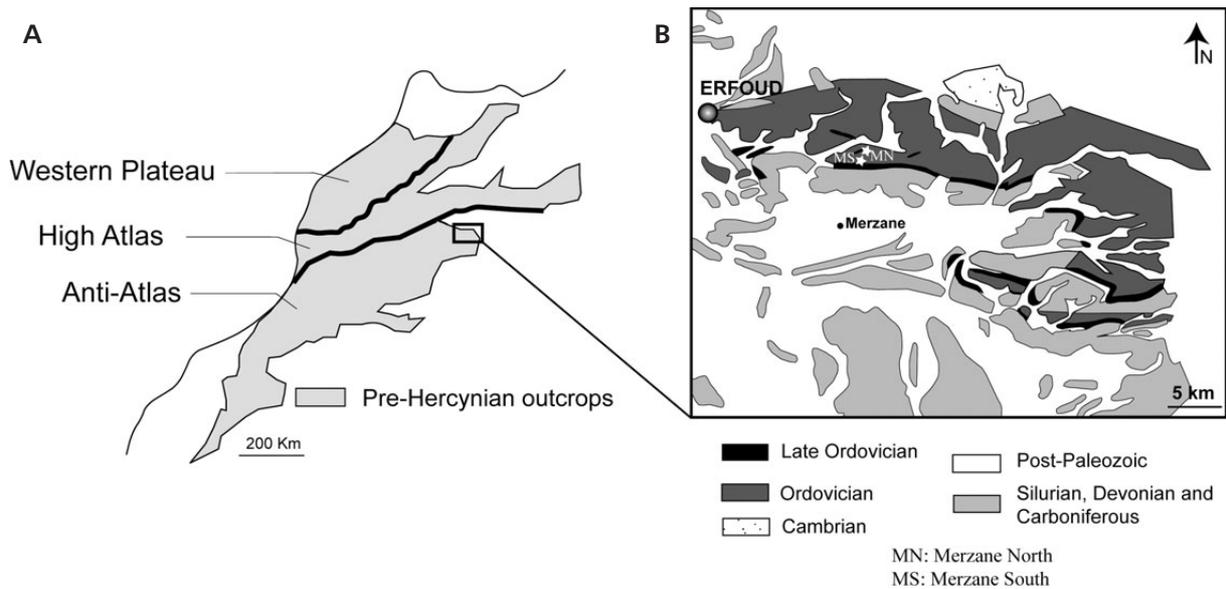


Figure 1. A – schematic geological map of the eastern area of Erfoud (Anti-Atlas, Morocco). • B – location of the studied stratigraphic section. Taken from Jiménez-Sánchez *et al.* (2015).

Recent studies on the bryozoans of the late Katian Khabt-el-Hajar Formation (Jiménez-Sánchez *et al.* 2015a, b), have identified 21 species of 12 trepostomate genera adapted to marly substrates of lower offshore environments, close to the Antarctic Polar Circle. Many of these species display significantly larger body sizes than congeneric species from lower latitudes, and several of them, based on their autozoocelial sizes, may be examples of polar gigantism. At the moment new bryozoans are being studied from the same Khabt-el-Hajar Formation, representing shallower environments than those previously collected. The studied horizons represent storm-induced deposits of upper offshore environments, as well as high-energy deposits typical of a shore face environment. Analysis of the bryozoan fauna has resulted in the addition of another 15 species of 13 genera, of which 10 have not been previously identified. Furthermore, genera assigned as Fenestrata and Cryptostomata have not been recognised in former studies of the region. This large number of bryozoans, now established from a reduced area of the Moroccan Anti-Atlas, has allowed reconsidering the palaeobiogeographic relationships of the region within the temperate-to-cool water Mediterranean Province during moments previous to the Hirnantian glaciation.

Geographical and geological setting

Merzane North (MN) and Merzane South (MS) are two studied sections near the locality of Erfoud, in the easternmost edge of the Moroccan Anti-Atlas (Fig. 1). During the Lower Palaeozoic the Erfoud area corresponded to a mixed

carbonate-siliciclastic platform with sharp lateral boundaries and is considered as an isolated platform (El Maazouz & Hamoumi 2007). It is represented by the Khabt-el-Hajar Formation (Destombes *et al.* 1985), consisting of two mixed siliciclastic limestone units separated by a mixed marl-limestone unit. A preliminary sedimentological and stratigraphical study of the succession was presented by Meddour *et al.* (2010), and a more detailed stratigraphical and sedimentological description can be found in Jiménez-Sánchez *et al.* (2015a). The studied bryozoans have been collected from three different horizons (MN4, MS1 and MS5), corresponding to the three sedimentary units described in the latter paper (Figs 2 and 3) and referred to above. Carbonate productivity was not laterally persistent in the eastern Anti-Atlas, as shown by Alvaro *et al.* (2007). In the Tskaouine and Gaiz Jebels of the Alnif area (Alvaro *et al.* 2007) and in the Western Tafilalt domain (El Maazouz & Hamoumi 2007) a siliciclastic-dominated platform records low activity of carbonate factories. These were known to be intensive in the Erfoud area as indicated by the bryozoan-dominated limestones of the late Katian Khabt-el-Hajar Formation.

Sedimentological patterns

The first unit (Unit 1; Fig. 2) of the bryozoan-rich Khabt-el-Hajar Formation overlaps the sandstones of the Upper Tiouririne Formation and is up to 40 m thick. Its basal part is characterised by mixed siliciclastic-limestone layers of several dm thick showing an erosional base, stacked inversely to normal graded cm to dm-thick bioclastic accumula-

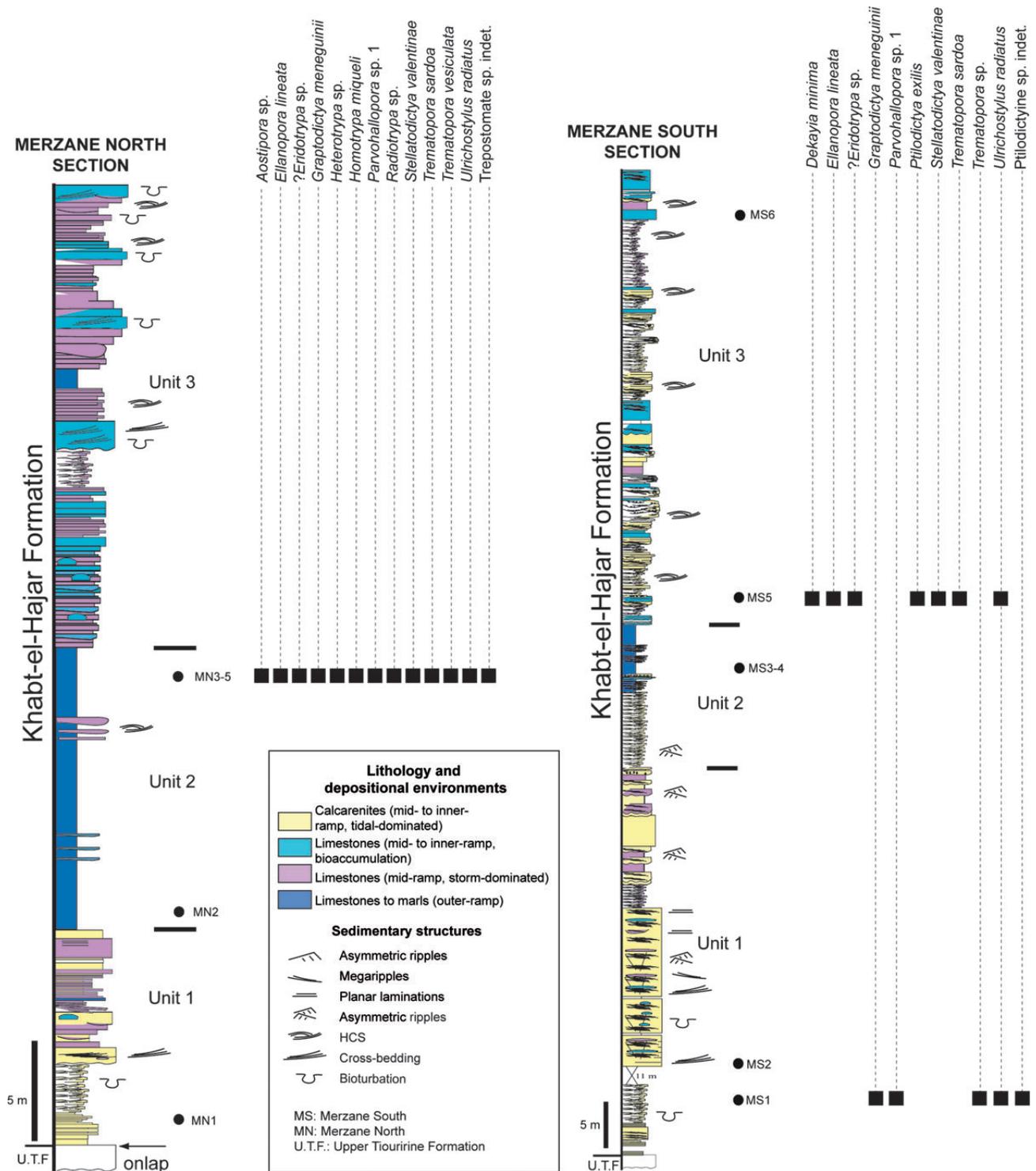


Figure 2. Stratigraphic log and distribution of the studied taxa in the Merzane North and Merzane South Sections. For the geographical location of horizons 3–5 (MN 3–5) in Merzane North Section see Jiménez-Sánchez *et al.* (2015), fig. 3.1.

tions composed of bryozoans and echinoderms and corresponds to storm-induced deposits of an upper offshore environment (horizon MS1). It passes upward to mixed limestone-siliciclastic sediments characterised by bidirec-

tional cross-beddings, asymmetrical to interference ripples and mud drapes, which correspond to tide-dominated deposits in a shoreface environment. The second unit (Unit 2) consists of marls and fine-grained limestones and is about

Table 1. Summary of the statistical analysis of *Enallopora lineata* Boulange, 1963, including: observed range (Or), mean value (X), standard deviation (SD), total number of measurements (Nm), and number of fragments on which measurements have been taken (Nsp). All measurements in mm.

Character	Or	X	SD	Nm	Nsp
Branch minimum diameter	0.32–1.00	0.59	0.21	9	9
Extrazooecial skeleton thickness	0.037–0.225	0.112	0.047	43	17
Pores diameter	0.025–0.050	0.039	0.009	9	3
Zooecial minimum diameter	0.09–0.17	0.14	0.02	18	6
Zooecial internal wall thickness	0.010–0.050	0.021	0.010	28	14
Zooecial minimum diameter in endozone	0.07–0.15	0.11	0.02	20	9
Zooecial spacing along branch	0.50–0.65	0.60	0.05	9	3

15 m thick both at the Merzane North and Merzane South sections. It is characterised by cm-thick inversely graded bioclastic units with an erosional base (horizon MN4) embedded in marls. These reworked bioclastic units are considered as tempestites deposited in upper offshore environments. The marls are devoided of storm-induced deposits, showing complete bryozoans studied in Jiménez-Sánchez *et al.* (2015a, b), and are interpreted as deposits of lower offshore environments. The third unit (Unit 3) is composed of pluri-dm to m-thick mixed siliciclastic-limestone layers (horizon MS5). Storm-induced deposits of upper offshore environment characterise this unit at Merzane North whereas at Merzane South it shows trough cross-beddings, thickening and fining upward succession, ripple marks and occasional storm-induced deposits (SCS – Swaley-cross-laminations) corresponding to high-energy mixed siliciclastic-limestone megaripples, deposited in a shoreface environment. The three horizons studied here, MN4, MS1, and MS5 correspond, therefore, to high-energy environments in which bryozoans with different degrees of fragmentation and transport were accumulated, most of them showing considerable superficial mechanical erosion.

Systematic palaeontology

Twenty-three thin sections with a total of 77 specimens have been studied in this systematic work using a transmitted light petrographic microscope. The measurements have been taken from the thin sections, either directly through the microscope with micrometer or from scaled photographs. In the following descriptions all average are mean values. Material described here is housed in the Museo de Ciencias Naturales of the University of Zaragoza (Spain) with catalogue numbers MPZ 2014/X and MPZ 2015/X, where “X” is the identification number for each specimen. These numbers appear in the description of the species. In Fig. 2 is shown the stratigraphic distribution and horizon where each taxon was collected.

Class Stenolaemata Borg, 1926
 Superorder Palaeostomata Ma *et al.*, 2014
 Order Fenestrata Astrova & Morozova, 1956
 Suborder Phylloporina Lavrentjeva, 1979
 Family Enalloporidae Lavrentjeva, 1985

Genus *Enallopora* d’Orbigny, 1850

Type species. – *Enallopora perantiqua* (Hall, 1847). Caradoc (Upper Ordovician) of Middleville, Herkimer County (New York, U.S.A.).

Diagnosis. – Following Ernst & Carrera (2012) *Enallopora* is characterized by having branched colonies dichotomously divided and not linked by either anastomoses or dissepiments; zooecia arranged in two or four longitudinal rows; median keel absent or poorly developed, and without spine or nodes. Zooecia consist of large tubes originating from and extending along planar wall of branch axial mid-plane. Zooecial apertures oval to rounded, often surrounded by small nodes. Peristome complete and long. Reverse and axial walls having microgranular structure and interzooecial skeleton finely laminated. Exozonal tubes present both to obverse and reverse surface, with rounded or oval openings.

Occurrence. – Middle Ordovician to Lower Silurian of North and South America, Europe, North Africa (Morocco) and India.

Enallopora lineata Boulange, 1963

Figure 3A, B, Table 1

1963 *Enallopora lineata* Boulange; Boulange, pp. 39–40, text-figs 5a, b.

Material. – MPZ 2014/494–510.

Description. – Branched colonies with an average minimum branch diameter of 0.59 mm. Zooecia budding from a central axis in two stages of two paired rows divided by a vertical lamina; in proximal part zooecia growth parallel to branch, but in distal part they sharply bend to become nearly perpendicular to zoarial surface. Zooecia quadrangular to round in endozone with an average diameter of 0.11 mm and separated by an internal wall of an average thickness of 0.021 mm with granular microstructure. Zooecial aperture oval in shape, sometime rounded, with a minimum average diameter of 0.14 mm; open to the obverse side and arranged in longitudinal rows, with spacing between them of 0.60 mm on average, measured longitudinally; apertures surrounded by a peristome with laminated microstructure. Extrazooecial skeleton thick (0.112 mm on average), with

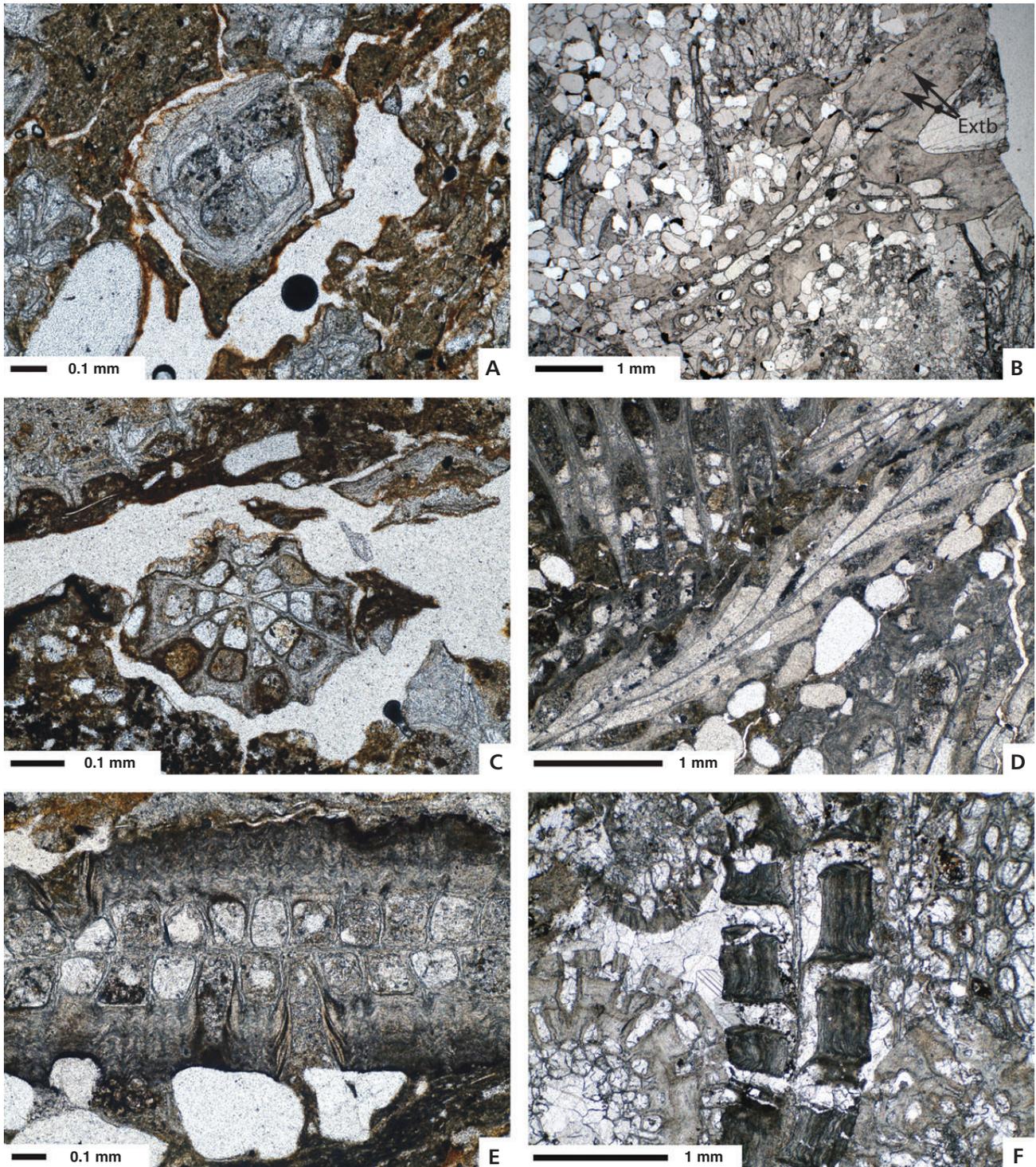


Figure 3. A, B – *Enallopora lineata* Boulange, 1963; A – transversal section of specimen MPZ 2014/494 showing quadrangular to round autozoecia in endozone; B – inclined section of specimen MPZ 2014/508 showing exozonal tubes (Extb). • C, D – *Ulrichostylus radiatus* Conti, 1990; C – transversal section of specimen MPZ 2014/511 showing triangular autozoecia in endozone and elliptical autozoecia in exozone; D – longitudinal section of specimen MPZ 2014/517 showing the lineal axis. • E, F – *Graptodictya meneghinii* (Vinassa de Regny, 1942); E – transversal section of specimen MPZ 2014/526 showing mesotheca, quadrangular autozoecia in endozone and thick laminated and crinkled extrazooecial skeleton; F – longitudinal section of specimen MPZ 2014/531. Specimens MPZ 2014/494, 511, 517 and 526 from horizon MN4; specimen MPZ 2014/531 from horizon MS1; and specimen MPZ 2014/508 from horizon MS5.

Table 2. Summary of the statistical analysis of *Ulrichostylus radiatus* Conti, 1990. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with central axis	10.5°–19.7°	14.7°	4.1	5	1
Autozooeccial angle with zoarial surface	19.0°–61.1°	36.5°	17.2	16	3
Autozooeccial aperture minimum diameter	0.12–0.15	0.14	0.01	4	1
Autozooeccial distal wall thickness in exozone	0.030–0.075	0.049	0.014	13	6
Autozooeccial minimum diameter in exozone	0.05–0.11	0.08	0.01	20	8
Autozooeccial rows	7–14	11	3	10	10
Autozooeccial wall thickness in endozone	0.009–0.020	0.014	0.004	21	8
Branch minimum diameter	0.47–1.17	0.80	0.25	10	10
Endozone minimum diameter	0.20–0.40	0.31	0.07	7	7

laminated microstructure, and crossed by numerous exozonal tubes, oval to rounded in shape and with an average diameter of 0.039 mm, present in both obverse and reverse sides.

Remarks. – The shape of the colonies with branches dichotomously divided and not linked by either anastomoses or dissepiments; the zooecia arranged in longitudinal rows; the absence of median keel; the zooecial tubes originating from and extending along planar wall of branch axial mid-plane, the oval to rounded zooecial apertures and the presence of peristome in the apertures; the reverse and axial walls with granular microstructure and the interzooecial skeleton finely laminated; and finally, the exozonal tubes present in both obverse and reverse surface, with rounded or oval openings, are the characters that have allowed us to include this material in the genus *Enallopora*.

This material has been assigned to *Enallopora lineata* defined by Boulange (1963) in the Upper Ordovician (Ashgill) of the Grange du Pin (Hérault, France) because the specimens are quantitatively and qualitatively very similar to this species. They share the way in which zooecia grow from the median wall, recumbent in the proximal part and forming a sharp angle with the external surface in the distal one; the zooecial apertures arranged in four longitudinal rows with the lateral adjacent apertures at different heights; the random distribution of the exozonal tubes in the obverse side; the minimum diameter of branch (0.59 mm in Moroccan material on average vs 0.50 mm in the French ones); and the minimum zooecial diameter (a range of 0.09–0.17 mm in Moroccan material vs 0.14–0.17 mm in the French ones).

Enallopora lineata can be distinguished from *E. exiqua* (Ulrich, 1890) described by this author in the Upper Ordovician of North America and by Ernst & Carrera (2012) in the Upper Ordovician of the Argentinean Precordillera because

the latter species has much smaller branch and zooecial diameters (a range of 0.27–0.47 mm in *E. exiqua* branch diameter vs 0.32–1.00 mm in *E. lineata* described in Morocco and a range of 0.05–0.10 mm in *E. exiqua* zooecial diameter vs 0.09–0.17 mm in *E. lineata* described in Morocco) and the distribution of the exozonal tubes is more regular than in *E. lineata*.

Occurrence. – This species has been described in the Ashgill (Upper Ordovician) of the Grange du Pin (Hérault, France) and in the Khabt-el-Hajar Formation, horizons MN4 and MS5, in the northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Order Cryptostomata Vine, 1884

Suborder Rhabdomesina Astrova & Morozova, 1956

Family Arthrostylidae Ulrich, 1882

Genus *Ulrichostylus* Bassler, 1952

Type species. – *Helopora divaricatus* Ulrich, 1886. Decorah Shale, Middle Ordovician of Minneapolis (USA).

Diagnosis. – Following Ernst & Key (2007) *Ulrichostylus* is characterized by having dendroid to unbranched colonies. Autozooeccial apertures arranged in 6–8 longitudinal rows, separated by prominent longitudinal ridges. Axial region formed by a lineal axis, where autozooeccia budding with an angle of 20°–40°. Autozooeccial cross-section triangular in endozone, becoming elliptical in exozone, forming an angle of 60°–70° with colony surface. Diaphragms rare or absent. Exozonal material well developed. Mesozooecia absent. Paurostyles scattered, weakly developed.

Remarks. – Blake (1983) revised the genus *Ulrichostylus* and reduced its number of autozooeccial rows from eight or more, as was considered by Bassler (1952), to between six and eight. Conti (1990) included *Ulrichostylus radiatus* with twelve autozooeccial rows in the genus *Ulrichostylus*. Ernst & Key (2007) considered again 6 to 8 as the diagnostic number of autozooeccial longitudinal rows. We follow Ernst & Key's (2007) diagnosis, but accept the increase in the number of autozooeccial rows introduced by Conti (1990).

Occurrence. – Middle to Upper Ordovician of North America, Europe and North Africa (Morocco).

Ulrichostylus radiatus Conti, 1990

Figure 3C, D, Table 2

1990 *Ulrichostylus radiatus* Conti; Conti, p. 116, pl. 21, figs 7–12.

- 2007 *Ulrichostylus radiatus* Conti, 1990. – Ernst & Key, p. 401, pl. 15, figs 1–4.
 2007 *Ulrichostylus* sp. Conti, 1990. – Jiménez-Sánchez et al., p. 685, fig. 8.2.
 2009 *Ulrichostylus radiatus* Conti, 1990. – Jiménez-Sánchez, pp. 698–699, fig. 10d, e.

Material. – MPZ 2014/511–525.

Description. – Zoarium ramose; individual branches sub-polygonal in cross-section with an average diameter of 0.80 mm. Autozooeical apertures large (0.14 mm of average diameter) and arranged in longitudinal rows (an average of 11 per branch), separated in this direction by a prominent ridge. Axial region formed by a well-defined linear axis, with autozooeica arranged radially around it. Endozone with an average diameter of 0.31 mm, with triangular autozooeica growing from the central axis with an average angle of 14.7°. In exozone autozooeica elliptical in cross-section with an average minimum diameter of 0.082 mm and reaching zoarial surface with an average angle of 36.5°. In endozone autozooeical walls hyaline, continuous from the central axis, with an average thickness of 0.014 mm; in exozone walls composed of a hyaline layer, sheathed by outer laminated skeleton; autozooeical distal wall in exozone 0.049 mm of average thickness.

Remarks. – The arrangement of autozooeical apertures in longitudinal rows separated by prominent ridges; the presence of the central axis with autozooeical rows around it; the shape of autozooeical cross-section both in endozone and exozone; as well as the absence of autozooeical diaphragms and mesozoeica have allowed us to assign this material to *Ulrichostylus*.

These specimens fit well with *Ulrichostylus radiatus* as was described by Conti (1990) in the Upper Ordovician type material from Sardinia (Italy), by Ernst & Key (2007) in the Upper Ordovician from the Montagne Noire (France) and by Jiménez-Sánchez (2009) in the Upper Ordovician of the Iberian Chains (Spain). The Moroccan material shares with them the absence of autozooeical diaphragms and acanthostyles, as well as a similar number of autozooeical rows and similar autozooeical diameter; consequently these specimens are included in *U. radiatus*.

Ulrichostylus radiatus is similar to *U. costatus* Lobdell, 1992, but the former species has more autozooeical longitudinal rows (7–14 in *U. radiatus* described in Morocco vs 7–8 in *U. costatus*) and smaller autozooeical apertures (0.12–0.15 mm in Moroccan *Ulrichostylus* vs 0.10–0.20 mm in *U. costatus*).

Occurrence. – This species has been described in materials from the Upper Ordovician (upper Katian) of: the Maciurru and Punta S'Argiola Members of the Domus-Novas For-

mation (Sardinia, Italy), the carbonate and clastic sequence from the Montagne Noire (France), the La Peña Member (layers 4, 6–9, 11 and 12) of the Valdelaparra section (Fombuena, Spain), and the Khabt-el-Hajar Formation in horizons MN4, MS1 and MS5, northeastern Moroccan Anti-Atlas (Morocco).

Suborder Ptilodictyina Zittel, 1880

Family Ptilodictyidae Zittel, 1880

Genus *Graptodictya* (Ulrich, 1882)

Type species. – *Graptodictya perelegans* (Ulrich, 1878). Waynesville Shale (Upper Ordovician of Ohio, U.S.A.).

Diagnosis. – Following Ernst & Key (2007) the genus *Graptodictya* is characterized by having bifoliate branching colonies; mesotheca slightly sinuous in longitudinal section and sometime zigzag in transverse ones; in the exozone autozooeica form an angle of 80°–90° with mesotheca; pustules abundant in the autozooeical boundaries, in the exozonal walls and in the extrazooeical skeleton; autozooeical cross-section elliptical to oval; superior hemisepta common, generally short and blunt and curving proximally; exilazoeica and monticules absent to rare; extrazooeical skeleton laminate, commonly crinkled forming longitudinal striae between autozooeica, along colonial margins and proximal parts of colonies.

Occurrence. – Middle Ordovician to Lower Silurian of Europe, North America and North Africa (Morocco).

Graptodictya meneghinii (Vinassa de Regny, 1942)

Figures 3E, F, 4A, Table 3

- 1942 *Pachydictya meneghinii* Vinassa de Regny; Vinassa de Regny, pp. 1030–1031, pl. 1, figs 6–8.
 1942 *Graptodictya* sp. Vinassa de Regny, 1942. – Vinassa de Regny, p. 1030, pl. 1, figs 4, 5.
 1942 *Pachydictya* (?) *sardoa* Vinassa de Regny, 1942. – Vinassa de Regny, p. 1031, pl. 1, fig. 11.
 1988 *Graptodictya* sp. (Vinassa de Regny, 1942). – Conti & Serpagli, p. 143, pl. 11, fig. 5, pl. 12, figs 2, 3.
 1990 *Graptodictya meneghinii* (Vinassa de Regny, 1942). – Conti, pp. 113–114, pl. 20, figs 4–7.
 2007 *Graptodictya meneghinii* (Vinassa de Regny, 1942). – Ernst & Key, p. 50, pl. 17, fig. 15, pl. 18, figs 1–3.
 2007 *Graptodictya* sp. (Vinassa de Regny, 1942). – Jiménez-Sánchez et al., p. 685, figs 7.5, 7.6.
 2009 *Graptodictya* cf. *meneghinii* (Vinassa de Regny, 1942). – Jiménez-Sánchez, pp. 690–692, fig. 3A, B, text-figs 4, 5.

Table 3. Summary of the statistical analysis of *Graptodictya meneghinii* (Vinassa de Regny, 1942). Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeical angle with mesotheca	29.0°–52.0°	40.1°	9.3	7	2
Autozooeical angle with zoarial surface	75.5°–89.5°	83.7°	5.4	6	2
Autozooeical aperture maximum diameter	0.19–0.30	0.23	0.03	16	3
Autozooeical aperture minimum diameter	0.09–0.17	0.11	0.02	17	3
Autozooeical diameter in endozone	0.09–0.15	0.12	0.01	24	3
Autozooeical spacing along branch	0.50–0.82	0.67	0.10	17	3
Autozooeical spacing diagonally	0.37–0.50	0.43	0.05	13	3
Autozooeical wall thickness in endozone	0.008–0.030	0.014	0.006	19	3
Autozooeical wall thickness in exozone	0.025–0.062	0.043	0.012	11	3
Brach thickness	0.70–0.90	0.76	0.08	5	5
Endozone thickness	0.11–0.19	0.13	0.02	16	4
Exozone thickness	0.14–0.35	0.24	0.05	17	5
Mesotheca thickness	0.012–0.037	0.021	0.008	15	5

Material. – MPZ 2014/526–535.

Description. – Bifoliate branch colonies with individual branches of 0.76 mm of average thickness. Autozooeia forming an initial angle of 40° with mesotheca, then they bend and grow parallel to mesotheca in endozone; autozooeical cross-section quadrangular to subcircular in endozone with an average diameter of 0.12 mm; in exozone autozooeia sharply bend forming an average angle of 84° with zoarial surface. Autozooeical apertures arranged in longitudinal rows with lateral adjacent apertures at different heights forming a diagonal pattern; oval to elliptical in shape with a minimum and maximum average diameter of 0.11 mm and 0.23 mm, respectively, and spacing 0.67 mm measured longitudinally and 0.43 mm measured diagonally. Autozooeical wall thin in endozone (0.014 mm of average thickness) and thicker in exozone (0.043 mm of average thickness) with laminated microstructure. Autozooeical aperture separated by a thick laminated and crinkled extrazooeical skeleton forming longitudinal striae between autozooeical apertures. Superior hemisepta present in distal part of autozooeia, short and blunt. Mesotheca lightly sinuous in longitudinal section and generally straight in transversal section, composed by two external laminated layer and a thin central one with granular microstructure; three-laminar mesotheca have a total thickness of 0.021 mm on average.

Remarks. – Material described here shares with the genus

Graptodictya the bifoliate habit of growth; the shape of mesotheca, slightly sinuous in longitudinal section; the angle that autozooeia form with mesotheca both in endozone and exozone; the elliptical to oval shape of autozooeical apertures; the short and blunt shape of superior hemisepta; as well as the laminated and crinkled thick extrazooeical skeleton, forming longitudinal striae between autozooeia. So, this material is assigned to *Graptodictya*.

Moroccan specimens are morphologically closely related to *G. meneghinii* (Vinassa de Regny, 1942), as described by Conti (1990) in the Upper Ordovician of Sardinia, and by Ernst & Key (2007) in the Upper Ordovician of Montagne Noire. They share the oval form of autozooeical apertures and its width (0.09–0.17 mm in Moroccan material, 0.08–0.16 mm in French material and 0.061–0.15 mm in Italian material) and the spacing of apertures along branch (0.50–0.82 mm in Moroccan material and 0.51–0.61 mm in the French one); the subpolygonal cross-section of autozooeia in endozone; the sharp autozooeical angle with the zoarial surface (always within the range of 75°–90°); the presence of short and blunt superior hemisepta; the presence of a thick laminated and crinkled extrazooeical skeleton; as well as the form of mesotheca, slightly sinuous in longitudinal sections and straight in transversal ones. So, these Moroccan specimens have been assigned to *G. meneghinii*.

Graptodictya lahgdadensis, Termier & Termier, 1950 was described in the basal mixed siliciclastic-carbonate unit of the Khabt-el-Hajar Formation (Jiménez-Sánchez *et al.* 2015a). No detailed description of this species is available, but in the hand-made drawings provided by Termier & Termier (1950) it is easy to distinguish *G. lahgdadensis* from *G. meneghinii* since the former has autozooeical diaphragms and sharp inferior hemisepta are present.

Occurrence. – This species has been described in the Ashgill (Upper Ordovician) of the Grange du Pin (Hérault, France); in the units *c* and *e* of the Upper Caradoc-Lower Ashgill (Upper Ordovician) of Sardinia (Italy) and in the Khabt-el-Hajar Formation, horizons MN4 and MS1, in the northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Genus *Ptilodictya* Lonsdale, 1839

Type species. – *Ptilodictya lanceolata* (Goldfuss, 1829). Wenlock (Silurian) of Great Britain.

Diagnosis. – Following Ernst & Carrera (2012) *Ptilodictya* is characterized by having colonies lancet or belt in shape; straight mesotheca, locally in zigzag, and without median rods; straight, tubular and long autozooeia, subrectangular to subhexagonal in endozone and commonly subrectangular

Table 4. Summary of the statistical analysis of *Ptilodictya exilis* Lavrentjeva, 1993. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeical aperture maximum diameter	0.29–0.37	0.34	0.03	12	1
Autozooeical aperture minimum diameter	0.10–0.14	0.12	0.01	12	1
Autozooeical spacing along branch	0.37–0.45	0.41	0.03	10	1
Autozooeical spacing laterally	0.12–0.20	0.17	0.02	10	1
Autozooeical wall thickness in endozone	0.005–0.012	0.009	0.004	5	1

in exozone, although oval form can be also present; autozooeical apertures arranged in longitudinal rows, separated by straight ridges; diaphragms absent; superior and inferior hemisepta as well as mural spines can be present; monticules flat to slightly raised and irregularly distributed.

Occurrence. – Middle Ordovician to Lower Devonian of North and South America, Europe, Siberia, Mongolia and India and Upper Ordovician of North Africa (Morocco).

***Ptilodictya exilis* Lavrentjeva, 1993
(in Gorjunova & Lavrentjeva 1993)**

Figure 4B, Table 4

1993 *Ptilodictya exilis* Lavrentjeva; Lavrentjeva in Gorjunova & Lavrentjeva, p. 68, pl. 10, fig. 4.

Material. – MPZ 2014/536.

Description. – Lancet bifoliate zoarium with maximum and minimum diameter unknown since no transversal section is available. Autozooeical apertures arranged in four longitudinal rows, separated by straight ridges, and spaced 0.41 mm longitudinally and 0.17 mm transversally (measured from centre to centre). Autozooeical cross-section subrectangular to oval in exozone, with a maximum and minimum average diameter of 0.34 mm and 0.12 mm, respectively; trapezoidal shape in cross-section near mesotheca. In endozone autozooeical apertures forming an angle of about 45° with mesotheca, constant up to zoarial surface. Autozooeical wall 0.009 mm of average thickness in endozone. Diaphragms, hemisepta and mural spines absent. Mesotheca is destroyed by compaction, therefore its morphology is unknown.

Remarks. – The lancet shape of the zoarium with the autozooeical apertures arranged in longitudinal rows, separated by straight ridges; the trapezoid autozooeical cross-section in endozone as well as the subbromboidal to oval shape in exozone; and the absence of diaphragms are characters pre-

sent in this Moroccan zoarium that have allowed us to include it in *Ptilodictya*.

The material described here shares with *Ptilodictya exilis* Lavrentjeva (in Gorjunova & Lavrentjeva, 1993), from the Caradoc (Upper Ordovician) of Estonia, the minimum diameter of autozooeical apertures (0.10–0.14 mm in the Moroccan material and 0.10–0.13 mm in the Estonian one), the subrectangular to oval autozooeical cross-section in exozone and the constant angle formed by autozooeical apertures from the mesotheca up to the zoarial surface. However, maximum autozooeical diameter is larger in Moroccan zoarium (0.29–0.37 mm vs 0.19–0.26 mm in the Estonian ones), but this difference in the diameter is largely caused by the inclined section of the Moroccan specimen. So, the Moroccan zoarium is assigned to *P. exilis*.

Occurrence. – This species has been described in the Caradoc (Jövi to Oandu stages: D_{I–III}) of Estonia and in the Khabt-el-Hajar Formation in the horizon MS5, northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Family Rhinodictyidae Ulrich, 1893

**Genus *Stellatodictya* Gorjunova, 1993
(in Gorjunova & Lavrentjeva 1993)**

Type species. – *Stellatodictya plana* Lavrentjeva in Gorjunova & Lavrentjeva, 1993. Caradoc (Upper Ordovician) of northwestern Russia.

Diagnosis. – Following Ernst & Key (2007) *Stellatodictya* is characterized by bifoliate colonies with flattened and ellipsoidal cross-section branches. Mesotheca straight and with median rods. Autozooeical growth parallel to mesotheca and strongly bend in internal exozone, without diaphragms or hemisepta. Autozooeical aperture rounded to oval with peristomes, arranged in diagonal rows. Interspace between autozooeical apertures consisting of vesicular tissue covered by a thick calcitic laminar skeleton. Vesicles large, having polygonal-box shape and curved roofs. Stellatopores developed in calcitic laminar skeleton, adjoined to autozooeical apertures and surrounding them in a single row. Without maculae.

Occurrence. – Upper Ordovician of northwestern Russia, Estonia, northern India, southern France and Morocco.

***Stellatodictya valentinae* Ernst & Key, 2007**

Figure 4C–E, Table 5

2007 *Stellatodictya valentinae* Ernst & Key; Ernst & Key, pp. 47–49, pl. 16, figs 12, 13, pl. 17, figs 1–6.

Table 5. Summary of the statistical analysis of *Stellatodictya valentinae* Ernst & Key, 2007. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	72.0°–86.0°	78.5°	4.8	13	3
Autozooeccial aperture minimum diameter	0.08–0.15	0.10	0.02	68	9
Autozooeccia/mm ²	8.0–15.0	11.2	2.0	12	6
Autozooeccial aperture spacing diagonally	0.20–0.45	0.32	0.06	24	5
Autozooeccial wall thickness in exozone	0.012–0.050	0.026	0.009	33	8
Extrazoeccial skeleton thickness	0.19–0.35	0.26	0.05	17	4
Number of autozooeccial rows in 5 mm diagonally measured	14–18	16	2	3	1
Stellathostyles diameter	0.025–0.100	0.053	0.015	31	7
Stellathostyles/mm ²	4–13	9	3	9	4

Table 6. Summary of the statistical analysis of *Ptilodictyine* sp. indet. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with mesotheca	23°–25°	24°	1	2	1
Autozooeccial angle with zoarial surface	52°–67°	57°	9	3	1
Autozooeccial diameter	0.10–0.15	0.12	0.02	5	1
Autozooeccial spacing along branch	0.45–0.57	0.51	0.06	3	1
Autozooeccial wall thickness	0.025–0.062	0.037	0.015	5	1
Mural styles diameter	0.012–0.030	0.023	0.006	7	1

Material. – MPZ 2014/537–545.

Description. – Bifoliate branching colonies with maximum and minimum branch diameter unknown since no transversal section has been obtained. Autozooeccial apertures rounded to oval with an average diameter of 0.10 mm and an average of 11.2 autozooeccia/mm²; arranged in diagonal rows with an average spacing of 0.32 mm between autozooeccial apertures and 16 rows/5mm in diagonal direction; autozooeccia growing recumbent on mesotheca; at base of exozone they bend sharply forming an average angle of 78.5° with zoarial surface; autozooeccial wall thin in endozone, without recognizable microstructure, at base of exozone wall thickens until reaching 0.026 mm of average thickness, with a laminated microstructure; autozooeccial diaphragms and hemisepta absent. Vesicles developed at base of exozone, having shape of quadrangular to rectangular boxes, with 1–2 rows of vesicles in longitudinal direction and 1–3 in horizontal direction; covered by calcitic laminated extrazoeccial skeleton with an average thickness of 0.26 mm. Stellathostyles large (0.053 mm of average diameter) and abundant (9 stellathostyles /mm²) and loca-

ted in laminated extrazoeccial skeleton; they are composed of a distinct light hyaline lumen with radially arranged rays, surrounded by sheaths. Macula absent.

Remarks. – The development of autozooeccia, growing parallel to mesotheca and strongly bend at the base of exozone; the absence of diaphragms and hemisepta; the shape of autozooeccial apertures and its arrangement in the zoarial surface; the presence of vesicular tissue between autozooeccia, that is covered by a laminated skeleton; the presence of stellathostyles located in the laminated skeleton; as well as the absence of macula are diagnostic characters that have allowed us to assign this material in the genus *Stellatodictya*. These specimens fit well with *Stellatodictya valentinae* Ernst & Key, 2007 as was described by the authors in the Upper Ordovician of the Montagne Noire (France), and accordingly they have been included in this species. They share, beside the diagnostic characters of the species, similar autozooeccial diameter (0.09–0.15 mm in the French material and 0.07–0.15 mm in the Moroccan material) and similar number of autozooeccial rows measured in diagonal direction (15–19 rows/5 mm in the French material and 14–18 rows/5 mm in the Moroccan material). The most noticeable difference between both materials is in the size of stellathostyles, smaller in the French material (0.01–0.03 mm vs 0.02–0.10 mm in the Moroccan material).

Occurrence. – This species has been described in the Upper Caradoc-Lower Ashgill of Montagne Noire (southern France), and in the Khabt-el-Hajar Formation in horizons MN4 and MS5, northeastern Moroccan Anti-Atlas, (Upper Ordovician, upper Katian).

Incertae sedis

Ptilodictyine sp. indet.

Figure 4F, Table 6

Material. – MPZ 2014/546.

Description. – Branch colony apparently bifoliate and with unknown diameter. Autozooeccia forming and initial angle of 24° with mesotheca, then they lightly bend and grow parallel to mesotheca in endozone; in exozone autozooeccia sharply bend forming an average angle of 57° with zoarial surface. Autozooeccial apertures apparently arranged in longitudinal rows, with a spacing of 0.51 mm along branch; autozooeccial cross-section circular with an average diameter of 0.12 mm. Autozooeccial walls laminated, 0.037 mm of average thickness in exozone. Mural styles abundant, 0.023 mm of average diameter and placed, as longitudinal rows, in skeletal material separating adjacent autozooeccial apertures.

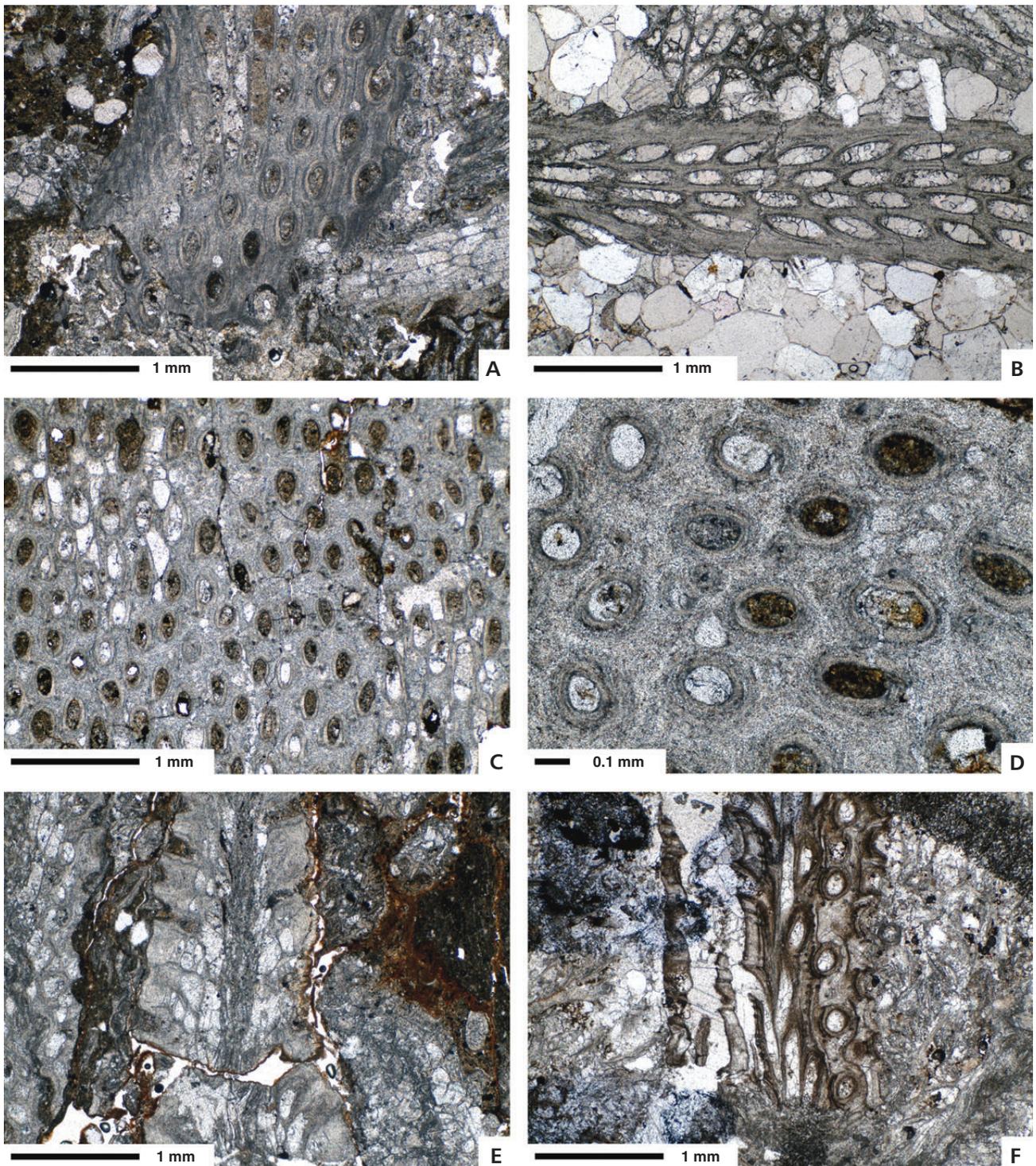


Figure 4. A – *Graptodictya meneghinii* (Vinassa de Regny, 1942), tangential section of specimen MPZ 2014/528. • B – *Ptilodictya exilis* Lavrentjeva, 1993, tangential section of specimen MPZ 2014/536. • C–E – *Stellatodictya valentinae* Ernst & Key, 2007; C – tangential section of specimen MPZ 2014/540; D – detailed deep tangential section of specimen MPZ 2014/539 showing stellathostyles and vesicles in exozone; E – longitudinal section of specimen MPZ 2014/542 showing numerous vesicles in exozone. • F – *Ptilodictyinae* sp. indet., inclined section of specimen MPZ 2014/546 showing numerous mural styles in extrazooecial skeleton. Specimens MPZ 2014/528, 539, 540 and 542 from horizon MN4; specimen MPZ 2014/546 from horizon MS1; and specimen MPZ 2014/536 from horizon MS5.

Table 7. Summary of the statistical analysis of *Radiotrypa* sp. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	38.0°–71.0°	49.0°	13.1	5	1
Autozooeccial diameter	0.10–0.14	0.12	0.01	8	3
Autozooeccial wall thickness in endozone	0.010–0.025	0.016	0.004	19	3
Autozooeccial wall thickness in exozone	0.030–0.060	0.045	0.009	11	3
Branch diameter	1.4–1.9	1.7	0.2	3	3
Endozone diameter	1.00–1.10	1.05	0.07	2	2
Exozone thickness	0.30–0.44	0.38	0.06	4	2

Remarks. – This specimen can be included in the suborder Ptilodictyina since it has a bifoliate zoarium and short autozooeccia growing from mesotheca. However, the scarcity of observed characters has precluded us to propose a more accurate systematic classification and we left it in open nomenclature to the generic level.

Occurrence. – Ptilodictyine sp. indet. is known exclusively from the Khabt-el-Hajar Formation, horizon MS1, northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Order Trepostomata Ulrich, 1882
 Suborder Amplexoporina Astrova, 1965
 Family Amplexoporidae Miller, 1889

Genus *Radiotrypa* Brood, 1978

Type species. – *Radiotrypa gothica* Brood, 1978. Hirnantian (Upper Ordovician) of Borenshult (Sweden).

Diagnosis. – Following Ernst *et al.* (2015) *Radiotrypa* is characterized by having branched colonies, with endozone and exozone well defined. Autozooeccia budding in 8–12 radial series from the central part of the branch, with 2–4 autozooeccial rows per series. Radial autozooeccial groups are separated by a layer produced by the thickening of autozooeccial walls in neighbouring series. Autozooeccial diaphragms rare to absent. Acanthostyles can be present. Exilazoeeccia present, rounded to polygonal in shape. Maculae not observed.

Radiotrypa sp.

Figure 5A, B, Table 7

Material. – MPZ 2015/1546–1548.

Description. – Ramose zoarium with an average branch

diameter of 1.7 mm; endozone 1.05 mm of average diameter and exozone 0.38 mm of average width. Autozooeccial apertures with an apparent diameter of 0.12 mm on average (measured in longitudinal sections); autozooeccial cross section irregularly polygonal in endozone, where they grow as long tubes parallel to branch axis; in internal exozone they gently bend forming an average angle of 49° with zoarial surface; arranged in 8 radial series separated by laminae that protrude as low ridges on colony surface, with 2–4 autozooeccial rows per series; diaphragms scarce, present in external endozone with no more than one or two per autozooeccium. Autozooeccial walls laminated, with an average thickness of 0.016 mm in endozone and 0.045 mm in exozone. Laminae separating autozooeccial radial series with laminar microstructure, thicker than autozooeccial walls in endozone but thinner in exozone. Exilazoeeccia and acanthostyles absent.

Remarks. – The arrangement of autozooeccia in radial series from the central part of the branch, with these series separated by a laminated layer produced by the thickening of autozooeccial walls in neighbouring series, together with the scarcity of autozooeccial diaphragms, have been the diagnostic characters that have allowed us to include these specimens in *Radiotrypa*.

Radiotrypa sp. described here can be easily distinguished from *R. alnifensis* Ernst *et al.*, 2015 (described in Ernst *et al.* 2015, in the Upper Ordovician glaciogenic deposits of Alnif, Morocco) because the latter has abundant exilazoeeccia and acanthostyles are present.

Occurrence. – *Radiotrypa* sp. is exclusive from the Khabt-el-Hajar Formation in the horizon MN4, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Family Heterotrypidae Ulrich, 1890

Genus *Heterotrypa* Nicholson, 1879

Type species. – *Monticulipora frondosa* d’Orbigny, 1850. Upper Ordovician (Cincinnatian) of North America.

Diagnosis. – Following Ernst & Key (2007) the genus *Heterotrypa* is characterized by its frondose, ramose or encrusting colonies with monticules generally composed of a small central cluster of mesozooeeccia. Autozooeccial diaphragms generally scarce in endozone and more abundant in exozone, where they are thin, planar, perpendicular to zooeeccial walls and regularly spaced; autozooeccial walls with variable thickness. Intermonticular mesozooeeccia range from abundant to absent; commonly develop moniliform chambers at proximal ends and tend to become smaller or are terminated distally within exozone; mesozooeeccial

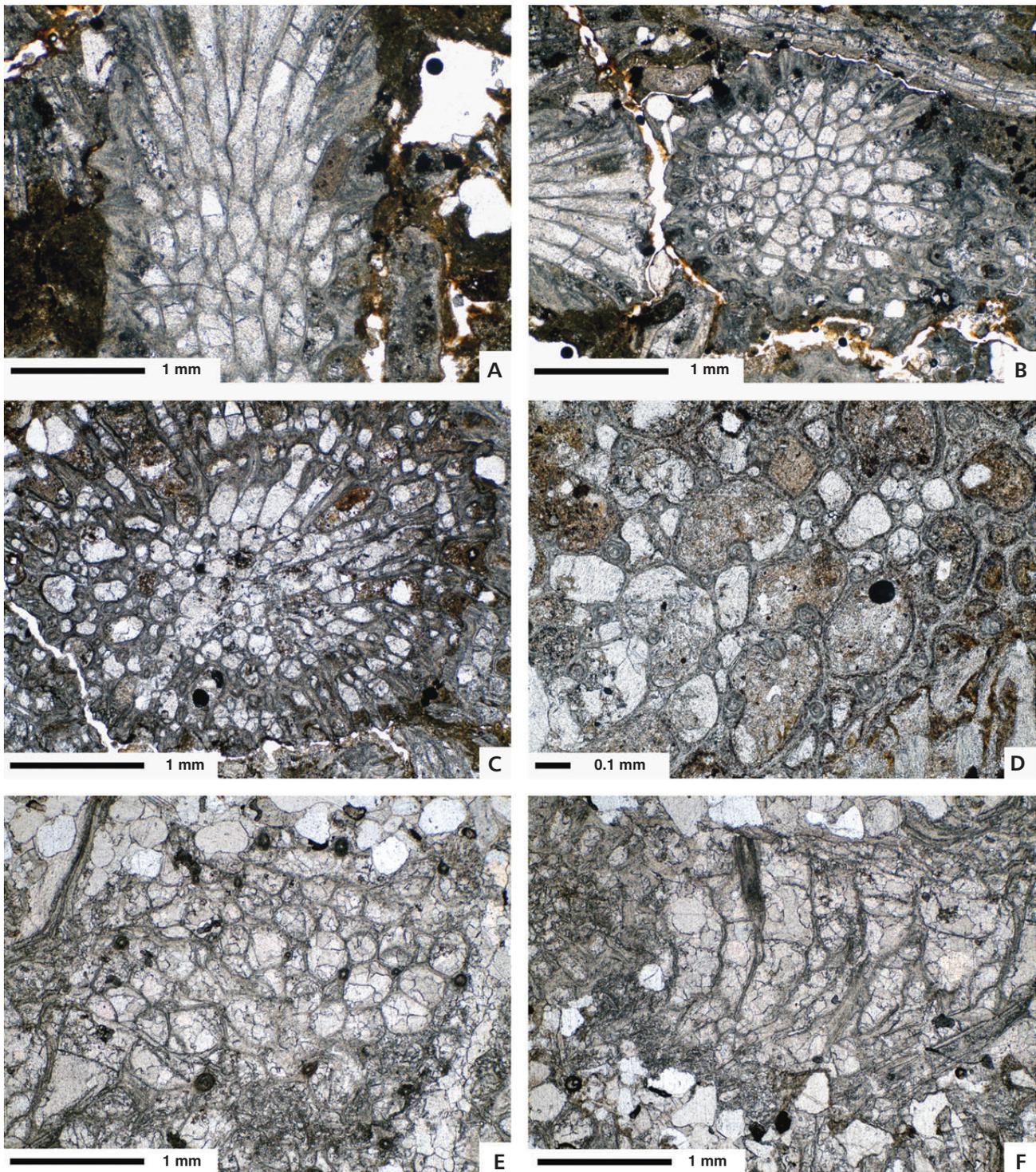


Figure 5. A, B – *Radiotrypa* sp., A – longitudinal section of specimen MPZ 2015/1547; B – transversal section of specimen MPZ 2015/1548. • C–D – *Heterotrypa* sp., specimen MPZ 2014/551; C – transversal section, and D – longitudinal section showing large acanthostyles modifying autozooeical cross-sections. • E, F – *Dekayia minima* Conti, 1990, specimen MPZ 2014/552; E – transversal section, and F – longitudinal section showing a large acanthostyle. Specimens MPZ 2014/551 and MPZ 2015/1547–1548 from horizon MN4; specimen MPZ 2014/552 from horizon MS5.

diaphragms thicker and more abundant than autozooeical diaphragms. Acanthostyles always present and differentiated into two types: regular acanthostyles limited

to exozone, and endacanthostyles originated in both endozone and exozone; only the latter are present in all species.

Table 8. Summary of the statistical analysis of *Heterotrypa* sp. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter	0.05–0.10	0.08	0.010	9	1
Acanthostyles/mm ²	21–25	22	2	3	1
Autozooeccial diameter	0.17–0.29	0.22	0.04	8	1
Autozooeccial apertures/mm ²	9–13	10	2	3	1
Autozooeccial wall thickness in endozone	0.007–0.012	0.011	0.002	5	1
Autozooeccial wall thickness in exozone	0.025–0.050	0.037	0.009	5	1
Branch minimum diameter	2.9	2.9	0	1	1
Endozone minimum diameter	1.7	1.7	0	1	1
Exozone thickness	0.67–0.75	0.70	0.05	2	1
Mesozooeccial diameter	0.07–0.12	0.10	0.02	8	1
Mesozooeccial apertures/mm ²	17–21	19	2	3	1

Occurrence. – This genus ranges from Middle Ordovician to Devonian and has a wide geographical distribution (North America, Europe, Asia and Northern Africa).

***Heterotrypa* sp.**

Figure 5C, D, Table 8

Material. – MPZ 2014/551.

Description. – Ramose zoarium with individual branches 2.9 mm in diameter (measured in only one transverse section); endozone 1.7 mm in diameter and exozone 0.70 mm of average width. Autozooeccial cross-section 0.22 mm of average diameter in exozone, irregularly rounded and generally indented by large acanthostyles, with an areal density of 10 apertures/mm²; throughout endozone autozooeccia are long tubes growing almost parallel to branch axis, in internal exozone they bend slightly, intersecting zoarial surface at a gentle angle; autozooeccial diaphragms scarce in endozone separated by three or more autozooeccial diameters, thin and perpendicular to zooeccial walls; diaphragms absent in exozone; autozooeccial walls with a microgranular structure in endozone, thin (0.01 mm of average thickness) and slightly wavy; in exozone they progressively thicken up reaching an average thickness of 0.037 mm, with laminated microstructure. Mesozooeccia abundant, developed in internal exozone, irregular in cross-section showing an average small diameter of 0.10 mm and an average areal density of 19 apertures/mm²; mesozooeccial diaphragms numerous, spaced less than one mesozooeccial diameter; thicker than autozooeccial diaphragms and perpendicular to mesozooeccial walls; mesozooeccia are slightly narrower where diaphragms join to walls. Acanthostyles present in endozone and exozone, large (0.08 mm of average diameter) and numerous

(22 acanthostyles/mm² of average), generally modifying autozooeccial cross-section; composed of a large hyaline core surrounded by dark laminated sheaths; there are no differences between acanthostyles and endacanthostyles.

Remarks. – The ramose colony, the presence of autozooeccial diaphragms in endozone and its shape, the mesozooeccial diaphragms thicker and more abundant than autozooeccial diaphragms, the moniliform chambers of mesozooeccia, as well as the presence of endacanthostyles both in endozone and exozone are characters present in the Moroccan zoarium and they have allowed us to include it in *Heterotrypa*. However, the presence of autozooeccial diaphragms is a character present in all species assigned to this genus and this character is absent in the material described here. Nevertheless, we include the Moroccan zoarium in *Heterotrypa* because it shows the most important diagnostic characters of the genus. This material does not allow the species identification and is not sufficient for establishing of a new species. Therefore, we left it in the open nomenclature.

Heterotrypa sp. can be distinguished from *H. magnopora* Boulange, 1963 from the Upper Ordovician of Montagne Noire (southern France), according the original diagnosis and subsequent description by Ernst & Key (2007), because the latter has numerous autozooeccial diaphragms, autozooeccia are larger (a range of 0.16–0.39 mm vs 0.17–0.29 mm in Moroccan zoarium) and acanthostyles are smaller (a range of 0.03–0.08 mm in French *Heterotrypa* vs 0.05–0.10 mm in the Moroccan species). *Heterotrypa* sp., described by Jiménez-Sánchez (2009) from the Upper Ordovician of Iberian Chains (Spain) is similar to the Moroccan material in size of autozooeccia, mesozooeccia and acanthostyles, but differs in presence of abundant autozooeccial diaphragms.

Occurrence. – This species is known exclusively from the Khabt-el-Hajar Formation, horizon MN4, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Genus *Dekayia* Milne-Edwards & Haime, 1851

Type species. – *Dekayia aspera* Milne-Edwards & Haime, 1851, Upper Ordovician of North America.

Diagnosis. – Following Ernst & Key (2007) the genus *Dekayia* is characterized by having ramose, encrusting or massive zoarium, generally with low monticules; autozooeccial diaphragms scarce, typically absent in endozone and widely sparse or even absent in exozone; zooeccial walls crenulated to undulating and irregularly thick in exozone; mesozooeccia rare or absent in intermonticular area; as well as acanthostyles present in endozone and exozone, placed mainly in zooeccial corners.

Occurrence. – Upper Ordovician of North America, Europe, North Africa and China and Lower Carboniferous of Russia.

***Dekayia minima* Conti, 1990**

Figure 5E, F, Table 9

1990 *Dekayia minima* Conti; Conti, p. 104, pl. 12, figs 4–6, pl. 13, fig. 8.

2007 *Dekayia minima* Conti, 1990. – Ernst & Key, p. 17, pl. 4, figs 12, 13.

Material. – MPZ 2014/552.

Description. – Massive zoarium with small number of megazooecia forming maculae. Autozooeical cross-section round to irregularly polygonal in exozone, with an average diameter of 0.26 mm and an average areal density of 9.5 apertures/mm²; diaphragms present only in some autozooeicia, but no more than two per autozooeicum, placed mainly in the distal part of tubes. Mesozooecia developed in exozone and irregularly polygonal in cross-section; with an average maximum diameter of 0.11 mm and an average areal density of 5.5 mesozooecia/mm²; diaphragms not observed. Acanthostyles large (0.072 mm of average diameter), but not abundant (3.5/mm² of average), developed in both endozone and exozone and placed in autozooeical corners; composed of a central hyaline core and dark sheaths surrounding it. Zooecial walls slightly undulating and with irregular thickness (0.010 mm of average thickness in exozone and slightly thinner in endozone).

Remarks. – The scarcity of autozooeical diaphragms and its complete absence in mesozooecia; the presence of large acanthostyles in autozooeical corners, both in endozone and exozone; and the undulated and irregular thickness of autozooeical walls are the characters that have allowed us to assign this specimen to the genus *Dekayia*.

This Moroccan zoarium has been assigned to *Dekayia minima* since it fits well with the description of this species made by Ernst & Key (2007) in the Upper Ordovician of the Montagne de Noire and Carnic Alps. Both materials share the massive habit of growth and have similar disposition of autozooeicia, mesozooecia and acanthostyles in the colonies; besides, the range of diameters of these structures is similar (for autozooeicia a range 0.19–0.30 mm in Moroccan zoarium vs 0.16–0.33 mm in French material; for mesozooecia a range of 0.08–0.15 mm in Moroccan zoarium vs 0.05–0.19 mm in French material; and for acanthostyles a range of 0.050–0.010 mm in Moroccan zoarium vs 0.050–0.080 mm in French material), so the Moroccan specimen is assigned to *D. minima*.

The Moroccan *D. minima* can be distinguished from the

Table 9. Summary of the statistical analysis of *Dekayia minima* Conti, 1990. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter	0.050–0.10	0.072	0.020	6	1
Acanthostyles/mm ²	3.0–4.0	3.5	0.7	2	1
Autozooeical aperture diameter	0.19–0.30	0.26	0.04	7	1
Mesozooeical diameter	0.08–0.15	0.11	0.03	5	1
Autozooeical wall thickness	0.007–0.012	0.010	0.002	8	1
Autozooeical apertures/mm ²	9.0–10.0	9.5	0.7	2	1
Mesozooeical apertures/mm ²	5.0–6.0	5.5	0.7	2	1

Moroccan *Dekayia* sp., described by Jiménez-Sánchez et al. (2015b), also in the Khabt-el-Hajar Formation, because *Dekayia* sp. has more regular polygonal autozooeicia, fewer mesozooecia (a range of 0.5–3.0/mm² in *Dekayia* sp. vs 5.0–6.0/mm² in *D. minima*), larger autozooeicia (a range of 0.29–0.43 mm in *Dekayia* sp. vs 0.19–0.30 mm in *D. minima*), more acanthostyles (a range of 1.2–10.7/mm² in *Dekayia* sp. vs 3.0–4.0/mm² in *D. minima*) and they are more irregular in longitudinal view.

Occurrence. – *Dekayia minima* is exclusive of the Upper Ordovician and has been described in the Upper Caradoc (unit *c*) of Sardinia (Italy), in the Ashgill of Montagne de Noire (southern France), in the siltstone/sandstone member of the Uggwa Formation (Caradoc to lower Ashgill of Italian Carnic Alps), and in the Khabt-el-Hajar Formation, horizon MS5 from the upper Katian of the eastern Moroccan Anti-Atlas.

Family Mesotrypidae Astrova, 1965

Genus *Homotrypa* Ulrich, 1882

Type species. – *Homotrypa curvata* Ulrich, 1882. Upper Ordovician of Cincinnati (USA).

Diagnosis. – Following Ernst & Key (2007) the genus *Homotrypa* is characterized by having ramose and frondose zoaria, sometimes encrusting and irregularly massive in the first stages. Autozooeical apertures polygonal, rounded to oval; autozooeical walls slightly thickened in exozone, with laminated microstructure; diaphragms more abundant in exozone than in endozone, where they can be absent, and cystiphagms only in exozone. Mesozooecia from scarce to abundant, sometimes clustering to form maculae. Acanthostyles abundant and small.

Occurrence. – This genus has a wide geographic range being present from the Middle Ordovician to the Lower Silurian in North America, North Africa, Europe, Australia and Siberia.

Table 10. Summary of the statistical analysis of *Homotrypa miqueli* (Prantl, 1940). Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	35°–66°	46°	14.2	6	1
Autozooeccial diameter	0.12–0.17	0.15	0.02	4	1
Branch minimum diameter	3.48	3.48	0	1	1
Endozone wall thickness	0.005–0.012	0.007	0.003	6	1
Exozone wall thickness	0.050–0.100	0.072	0.021	4	1

***Homotrypa miqueli* (Prantl, 1940)**

Figure 6A, B, Table 10

1940 *Homotrypella miqueli* Prantl; Prantl, pp. 93–94, pl. 1, fig. 6, pl. 2, figs 8, 9.

2007 *Homotrypa miqueli* (Prantl, 1940). – Ernst & Key, p. 14, pl. 3, figs 9–13.

Material. – MPZ 2014/553.

Description. – Ramose colony with a branch diameter of 3.5 mm and autozooeccial average diameter of 0.15 mm in exozone (measured in longitudinal section). In endozone autozooeccia have long tubes developed parallel to branch axis and with irregular diameter; in internal exozone they gently bend until reaching zoarial surface with an average angle of 46°. Autozooeccial diaphragms scarce in endozone, more numerous in endozone-exozone transit and scarce in external exozone; straight in shape, but curved and even sinusoidal forms are also present. Cystiphragms throughout exozone, covering only one side of autozooeccial walls (side facing branch axis), and irregular in size within the same autozooeccium. Mesozooecia not observed. Acanthostyles scarce, developed inside autozooeccial walls in external exozone. Autozooeccial walls thin in endozone (0.007 mm of average thickness) and with granular microstructure; in exozone with laminated microstructure and an average thickness of 0.072 mm.

Remarks. – This specimen fits well in the genus *Homotrypa* since it shares the ramose zoarium; the autozooeccial walls thickened in exozone, with laminated microstructure; the presence of diaphragms, more abundant in exozone than in endozone; the presence of cystiphragms only in exozone; and the presence of small acanthostyles. The only diagnostic character that has not been seen in the Moroccan material is the presence of mesozooecia, but we only have one specimen and it is possible that the absence of mesozooecia in this specimen is a consequence of the random longitudinal section.

The described characters of this *Homotrypa* fit well with the description of *H. miqueli* made by Ernst & Key (2007) in the Upper Ordovician of Montagne Noire

Table 11. Summary of the statistical analysis of *Aostipora* sp. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	80°–89°	86°	3	6	1
Autozooeccial maximum diameter	0.14–0.25	0.18	0.03	19	2
Autozooeccial minimum diameter	0.07–0.15	0.11	0.02	25	3
Autozooeccial cingulum thickness	0.020–0.037	0.027	0.004	14	2
Autozooeccia wall thickness in endozone	0.006–0.010	0.007	0.002	12	3
Branch minimum diameter	3.8–4.2	4.0	0.3	2	2
Endozone minimum diameter	2.85–2.92	2.89	0.05	2	2
Exozone thickness	0.45–0.57	0.52	0.04	6	2

(France) and it is included in this species. In both materials autozooeccia reach zoarial surface with similar angle, diaphragms and cystiphragms have the same distribution and similar shape; endozone and exozone autozooeccial walls are similar in thickness (endozone: 0.006–0.010 mm in French material and 0.005–0.012 mm in Moroccan one; exozone: 0.054–0.100 mm in French material and 0.050–0.100 mm in Moroccan one). However the autozooeccial diameter is different (0.11–0.25 mm in French material vs 0.12–0.17 mm in Moroccan one), but this difference can be explained by the fact that in Moroccan specimen this character has been measured in longitudinal section.

Homotrypa miqueli can be distinguished from *H. aff. alta* Cumings & Galloway, 1913 described by Jiménez-Sánchez (in Jiménez-Sánchez *et al.* 2015a), both in the same formation, because the former have smaller autozooeccial aperture (0.12–0.17 mm vs 0.17–0.46 mm in *H. aff. alta*), smaller cystiphragms, fewer acanthostyles and mesozooecia are absent in *H. miqueli* as described here.

Occurrence. – *Homotrypa miqueli* has been described in the Upper Ordovician (Caradoc to Ashgill) of the Montagne Noire (France); in the Uggwa Formation, siltstone and sandstone member (Upper Caradoc to Lower Ashgill) of the Carnic Alps (Italy); and in the Khabt-el-Hajar Formation in the horizon MN4, northeastern Moroccan Anti-Atlas, (Upper Ordovician, upper Katian).

Family Trematoporidae Miller, 1889

Genus *Aostipora* Vinassa de Regny, 1921

Type species– *Aostipora cystata* (Bassler, 1911), Middle Ordovician of Estonia.

Diagnosis. – Following Jiménez-Sánchez in Jiménez-Sánchez *et al.* (2015b), *Aostipora* is characterized by having

ramose zoarium with long autozooezia growing parallel to the branch axis in endozone and curving in exozone to form an angle of up to 90° with the zoarial surface. Autozooezial cross-section irregularly polygonal in endozone and rounded-polygonal or oval in exozone. Autozooezial diaphragms scarce or absent in endozone and exozone. Autozooezial walls thin in endozone and progressively thicker in exozone, showing a distinct fine lamination. Mesozoezia present, partitioned by both diaphragms and cysts in the same mesozoezium, and sometimes also filled with vesicular tissue; usually mesozoezia are covered by calcitic deposits in the external exozone. Acanthostyles rare or lacking.

Occurrence. – Middle Ordovician of Estonia (Kuckers Shale, Sandbian), Argentina (San Juan Formation, Sandbian), and Upper Ordovician of North Africa.

***Aostipora* sp.**

Figure 6C, D, Table 11

Material. – MPZ 2014/554–556.

Description. – Ramose zoaria with individual branches 4.0 mm of average diameter. Autozooezial aperture oval to subcircular, with average maximum and minimum diameters of 0.18 mm and 0.11 mm, respectively, and surrounded by a thick cingulum of 0.027 mm of average thickness; separation between adjacent autozooezia is generally larger than its minimum diameter and this space is occupied by calcitic deposits. Autozooezia irregularly polygonal in endozone; here they grow parallel to branch axis and curve gently in external endozone; at the base of exozone autozooezial curvature becomes stronger, forming an average angle of 86° with zoarial surface. Autozooezial diaphragms only present in some autozooezia, both in endozone and exozone and with a large separation between consecutive diaphragms. Autozooezial walls slightly undulated, thin in endozone (0.007 mm of average thickness) and not distinguishable from the cingulum in exozone. Mesozoezia originate in internal exozone and only visible in longitudinal section; their proximal parts are filled by vesicular structures that are covered by calcitic laminar deposit in external exozone. Exozone poorly developed (0.52 mm of average thickness); endozone 2.89 mm of average diameter. Acanthostyles absent.

Remarks. – The ramose zoarial growth habit, with long autozooezia growing parallel to the branch axis in endozone and curving in exozone to form sharply angle with the zoarial surface; the shape of autozooezial cross section both in endozone and exozone, the scarcity of autozooezial diaphragms; and especially the presence of numerous me-

sozooezia filled with calcitic deposits, that prevent seeing them in the external colonial surface, and the presence of vesicular structures inside these mesozoezia have allowed us to include this material in the genus *Aostipora*. But, the described material does not fit well with any known *Aostipora* species and it is insufficient for establishing of a new species, so we left it in open nomenclature to the species level.

Aostipora sp. differs from *A. elongata* Jiménez-Sánchez in Jiménez-Sánchez et al. (2015b), described also in the Khabt-el-Hajar Formation, in the absence of elongated-flattened macula composed of a calcitic deposit, in the lack of tubules (not real acanthostyles), and in the smaller exozone/endozone ratio (0.18 in *Aostipora* sp. vs 0.36 in *A. elongata*).

Occurrence. – *Aostipora* sp. is known exclusively from the Khabt-el-Hajar Formation, horizon MN4, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Genus *Trematopora* Hall, 1852

Type species. – *Trematopora tuberculosa* Hall, 1852, Lower Silurian of North America.

Diagnosis. – Following Ernst & Key (2007) *Trematopora* is characterized by having branched colonies; autozooezial apertures oval to rounded and with peristome, autozooezial diaphragms scarce and often absent in endozone; mesozoezia numerous and densely tabulated by diaphragms, with thin walls and beaded in internal exozone; near surface mesozoezial walls become thicker and in zoarial surface mesozoezial apertures are completely cover by calcitic laminated skeleton; acanthostyles abundant, often arranged near peristome or in mesozoezial walls.

Occurrence. – Upper Ordovician to Upper Silurian of Europe, North America and Asia, as well as Upper Ordovician of North Africa. Some species have been also described in the Middle Devonian of Europe and North America, as well as in the Lower Carboniferous of North America.

***Trematopora sardoa* (Vinassa de Regny, 1942)**

Figure 6E, F, Table 12

- 1942 *Leptotrypella? sardoa* Vinassa de Regny; Vinassa de Regny, pp. 1039–1040, pl. 3, figs 9–12.
- ?1950 *Trematopora clariondi* (Vinassa de Regny, 1942). – Termier & Termier, p. 16, 19, pl. 64, figs 9–15.
- 1963 *Trematopora hirsuta* (Vinassa de Regny, 1942). – Boulange, pp. 38–39, pl. 1, fig. 5a, b.
- 1990 *Trematopora sardoa* (Vinassa de Regny, 1942). – Conti, pp. 95–96, pl. 4, figs 7, 8, pl. 5, figs 1–4.

Table 12. Summary of the statistical analysis of *Trematopora sardoa* (Vinassa de Regny, 1942). Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter	0.037–0.087	0.064	0.016	10	2
Acanthostyles/mm ²	16–40	27	8	7	2
Autozooeccial angle with zoarial surface	44°–76°	62°	12	7	2
Autozooeccial maximum diameter	0.14–0.20	0.16	0.02	10	2
Autozooeccial minimum diameter	0.07–0.12	0.10	0.01	10	2
Autozooeccial wall thickness in exozone	0.020–0.030	0.026	0.003	10	2
Autozooeccia/mm ²	10.0–16.0	12.7	2.7	6	2
Branch minimum diameter	3.4	3.4	0	1	1
Endozone minimum diameter	2.0	2.0	0.0	1	1
Exozone thickness	0.68–0.81	0.75	0.06	3	1

2007 *Trematopora sardoa* (Vinassa de Regny, 1942). – Ernst & Key, pp. 29–30, pl. 9, figs 8–11.

Material. – MPZ 2014/562–566.

Description. – Ramose zoaria with individual branches 3.4 mm of diameter (measured in only one transversal section); endozone 2.0 mm of diameter and exozone 0.75 mm of average width. Autozooeccial cross-section oval in exozone, with average maximum and minimum diameters of 0.16 mm and 0.10 mm, respectively, and an average of 12.7 autozooeccia/mm²; in endozone autozooeccia are long tubes growing parallel to branch axis; in internal exozone they strongly bend, forming an average angle of 62° with zoarial surface. Autozooeccial walls thin in internal endozone, slightly undulated and without distinguishable microstructure; in external endozone they progressively thickened until reaching an average thickness of 0.026 mm in external exozone, showing a clear laminated microstructure. Autozooeccial diaphragms scarce, straight in shape, and present only in internal exozone. Mesozooeccia abundant, developed in external endozone, but only visible in longitudinal section since they are covered by a thick laminated calcitic deposit; no more than two or three diaphragms per mesozooeccia, straight or slightly curve. Acanthostyles large (0.064 mm of average diameter) and numerous (27/mm²); composed of a large hyaline lumen surrounded by dark concentric sheaths; they appear in external exozone and are located near autozooeccial walls, but without modifying them.

Remarks. – The oval shape of autozooeccial apertures; the scarcity of autozooeccial diaphragms; the abundance of mesozooeccia covered by calcitic deposits in the zoarial surface; as well as the large size and number of acanthostyles have allow us to include this material in the genus *Trematopora*. *Trematopora sardoa* is the most common species of *Trematopora* in the Mediterranean region and these spe-

cimens have been included in this species since they show its diagnostic characters (average size of the colonies and its polymorphs, oval autozooeccial apertures, scarcity of autozooeccial diaphragms and abundance of mesozooeccia).

Trematopora filalensis Termier & Termier, 1950 and *T. clariondi* Termier & Termier, 1950 were also described in the horizon Blue Limestones of the Khabt-el-Hajar Formation. The authors provided some statistical data and some schematic pictures of these species, but they did not describe them in detail. Based on these pictures, *T. filalensis* can be distinguished from *T. sardoa* as described here because the former has circular to oval autozooeccial apertures and autozooeccial diaphragms are present in endozone. However, the pictures of *T. clariondi*, as well as the statistical data (except for the branch diameter), show that it is very similar to our material and to the material of other regions assigned to *T. sardoa*. We are quite sure that *T. clariondi* is a junior synonymous of *T. sardoa*, but it has been impossible for us to examine Termier & Termier's (1950) material, since it is private and its storage location is unknown.

The material assigned here to *Trematopora sardoa* can be distinguished from *T. gracile* Ernst & Key, 2007 and *T. acanthostylita* Jiménez-Sánchez, 2009 (the other two *Trematopora* species described in the Mediterranean region) because *T. gracile* has autozooeccial diaphragms in the endozone and acanthostyles develop from the internal exozone. From *T. acanthostylita* can be distinguished because in this species the autozooeccial apertures are completely inflected by the acanthostyles.

Occurrence. – This species has been described in the Upper Caradoc-Lower Ashgill of Montagne Noire (southern France), in the Upper Caradoc-Lower Ashgill (units c and e) of Sardinian (Italy), and in the Khabt-el-Hajar Formation in horizons Blue Limestones, MN4 and MS5, northeastern Moroccan Anti-Atlas, (Upper Ordovician, upper Katian).

***Trematopora vesiculata* sp. nov.**

Figure 7A–C, Table 13

Type species. – Holotype: MPZ 2014/568. Paratypes: MPZ 2014/567 and MPZ 2014/569.

Type horizon and locality. – Merzane North section, horizon 4. Upper Katian (Upper Ordovician) of Morocco.

Material. – MPZ 2014/567–569.

Etymology. – After the presence of vesicular tissue in mesozooeccia.

Diagnosis. – *Trematopora* characterized by the presence of thick vesicular tissue in mesozooeccia.

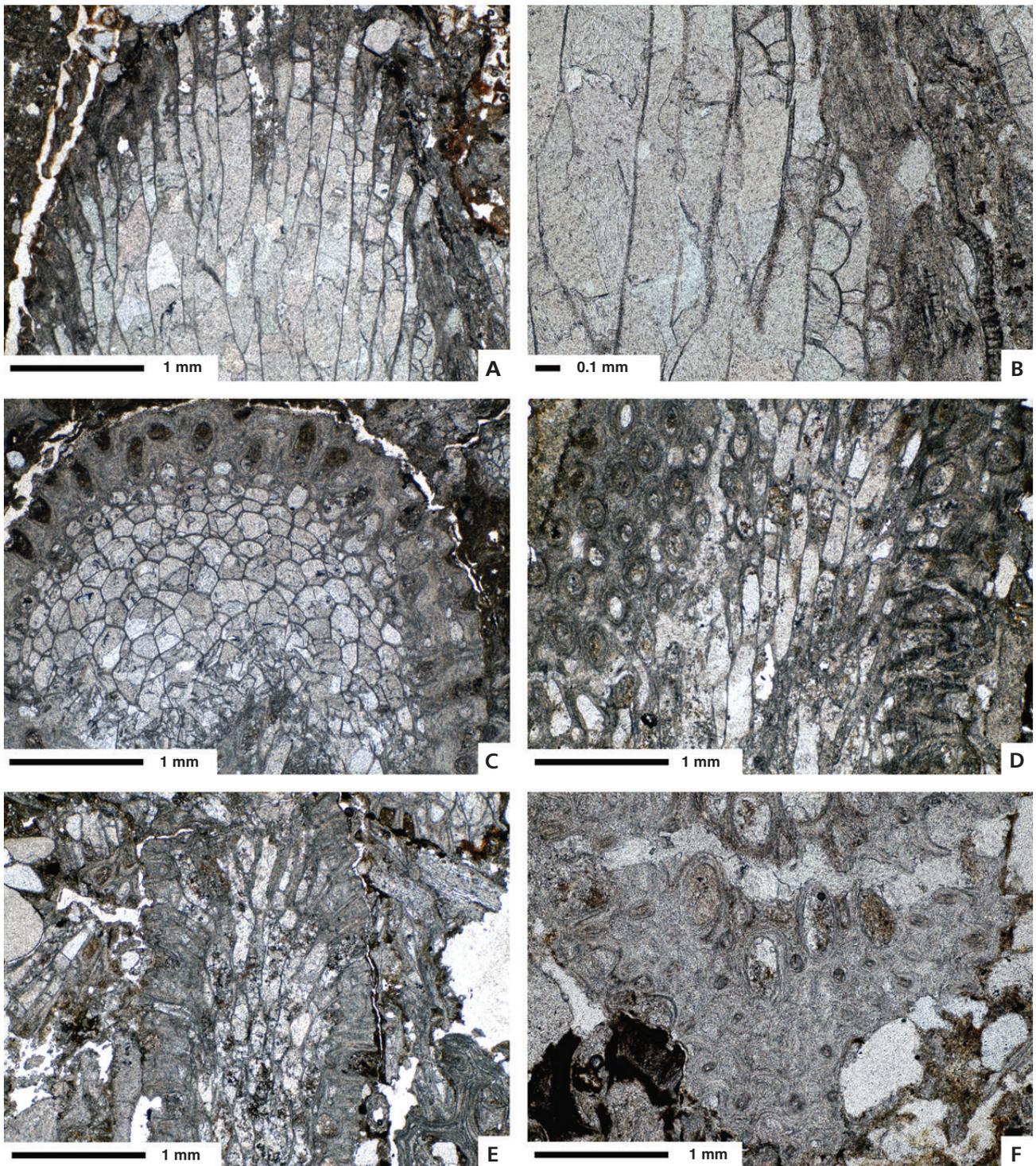


Figure 6. A, B – *Homotrypa miqueli* (Prantl, 1940), longitudinal sections of specimen MPZ 2014/553. • C, D – *Aostipora* sp.; C – transversal section of specimen MPZ 2014/555; D – inclined section of specimen MPZ 2014/554. • E, F – *Trematopora sardoa* (Vinassa de Regny, 1942), specimen MPZ 2014/563; E – longitudinal section, and F – tangential section showing large acanthostyles. All specimens from horizon MN4.

Description. – Ramose zoaria with individual branches 3.8 mm (measured only in one transversal section); endozone 2.3 mm in diameter and exozone 0.76 mm of average

width. Autozooeical cross-section rounded to slightly oval in exozone, with an average diameter of 0.12 mm; in endozone autozooeia are long tubes growing parallel to branch

Table 13. Summary of the statistical analysis of *Trematopora vesiculata* sp. nov. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter	0.050–0.125	0.076	0.021	19	3
Autozooeccial angle with zoarial surface	72.0°–86.0°	79.4°	4.3	7	2
Autozooeccial aperture diameter	0.10–0.16	0.12	0.02	18	3
Autozooeccial wall thickness	0.020–0.030	0.025	0.002	8	1
Branch thickness	3.8	3.8	0	1	1
Endozone diameter	2.3	2.3	0	1	1
Exozone width	0.75–0.80	0.76	0.02	4	1

Table 14. Summary of the statistical analysis of *Trematopora* sp. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Acanthostyles diameter	0.025–0.05	0.037	0.009	5	2
Autozooeccial angle with zoarial surface	59°–90°	77°	13	7	2
Autozooeccial minimum diameter	0.07–0.12	0.10	0.02	10	2
Autozooeccial wall thickness	0.025–0.040	0.033	0.006	7	2
Exozone thickness	0.37–0.55	0.49	0.05	7	2

axis; in internal exozone they strongly bend, forming an average angle of 79.4° with zoarial surface. Autozooeccial walls thin in internal endozone, without distinguishable microstructure; in external endozone they progressively thicken until reaching an average thickness of 0.025 mm in external exozone, with a clear laminated microstructure. Autozooeccial diaphragms present only in some tubes, but no more than one per autozooeccium; when present, they are straight, thick and placed in endozone or exozone. Mesozooecia abundant, developed in internal exozone, but only visible in longitudinal section since they are covered by a thick laminated calcitic deposit; mesozooecial diaphragms scarce, but thick when present; most part of mesozooecial tube filled by vesicular tissue and calcitic deposit. Acanthostyles large, 0.076 mm of average diameter, and no more than two per autozooeccium; composed of a large hyaline lumen surrounded by dark concentric sheaths; they start in internal exozone and are located near autozooeccial walls, but without modifying them.

Remarks. – The rounded shape of autozooeccial apertures; the scarcity of autozooeccial diaphragms, absent in most autozooeccia; the abundance of mesozooecia covered by calcitic deposits in the zoarial surface; the large size of acanthostyles; as well as the microstructures of zooeccial walls have allow us to assign this material to the genus *Trematopora*. However, no *Trematopora* species has been described as having the thick vesicular tissue observed in these Moroccan specimens. So, we define the new species *Trematopora vesiculata* to include them.

Trematopora vesiculata can be easily distinguished from *T. sardoa*, previously described, because the latter does not have vesicular tissue in mesozooecia, acanthostyles are more abundant and smaller in diameter (a range of 0.037–0.087 mm in *T. sardoa* vs 0.050–0.125 mm in *T. vesiculata*) and autozooeccia reach the zoarial surface at a less sharp angle (a range of 44°–76° in *T. sardoa* vs 72°–86° in *T. vesiculata*). The new species can be distinguished from *T. filalensis* Termier & Termier, 1950 because the latter lacks vesicular tissue in mesozooecia.

Occurrence. – This species is exclusive from the Khabtel-Hajar Formation, horizon MN4, in the northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

***Trematopora* sp.**

Figure 7D, E, Table 14

Material. – MPZ 2014/570–571.

Description. – Ramose zoarium, with exozone 0.49 mm of average width. Autozooeccial cross-section subcircular in exozone, with an average diameter of 0.10 mm; in endozone autozooeccia are long tubes growing parallel to branch axis, in internal exozone they bend abruptly forming an average angle of 77° with zoarial surface. Autozooeccial walls thin in endozone, slightly undulated and without distinguishable microstructure; in internal exozone they began thickening until reaching 0.033 mm of average thickness near zoarial surface, with a clear laminated microstructure. Autozooeccial diaphragms can be present in endozone and exozone, but no more than one or two per autozooeccium, straight in shape. Mesozooecia abundant, one or two rows separating each autozooeccium, developed in internal exozone when autozooeccia bend; only visible in longitudinal section since they are covered by a thick laminated calcitic deposit; mesozooecial diaphragms scarce and extremely thick. Acanthostyles numerous and with an average diameter of 0.037 mm; composed of a hyaline lumen surrounded by dark concentric sheaths; they appear at different depths in exozone and are located mainly between mesozooecia.

Remarks. – The subcircular shape of autozooeccial apertures, the scarcity of autozooeccial diaphragms, the abundance of mesozooecia covered by skeletal deposits in the zoarial surface, as well as the large number of acanthostyles have allow us to include this material in the genus *Trematopora*. However these specimens do not fit well in any of the known *Trematopora* species. It could be a new species, but we do not have the appropriate sections to define it. So, we leave these specimens in open nomenclature to the species level.

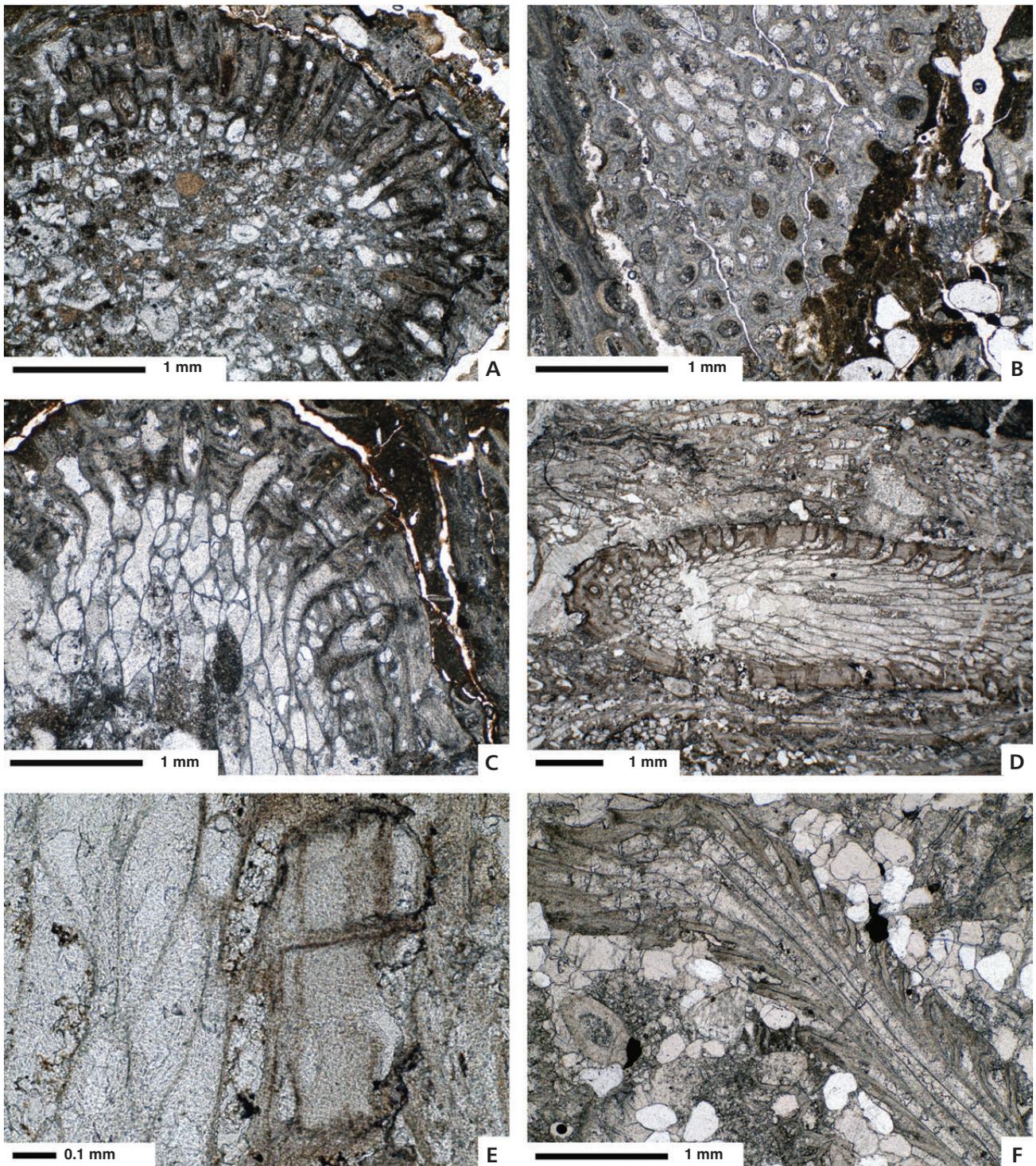


Figure 7. A–C – *Trematopora vesiculata* sp. nov.; A – transverse section of specimen MPZ 2014/569; B – tangential section of specimen MPZ 2014/567; C – longitudinal section of specimen MPZ 2014/568 (holotype); in Figs A and C is shown vesicular tissue in mesozooecia. • D, E – *Trematopora* sp.; D – longitudinal section of specimen MPZ 2014/571; E – detailed longitudinal section of specimen MPZ 2014/570 showing large acanthostyles. • F – *?Eridotrypa* sp. longitudinal section of specimen MPZ 2014/560. Specimens MPZ 2014/567–569 from horizon MN4; specimens MPZ 2014/570–571 from horizon MS1; specimen MPZ 2014/560 from horizon MS5.

Table 15. Summary of the statistical analysis of *?Eridotrypa* sp. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	18°–36°	26°	6	10	4
Autozooeccial diameter	0.15–0.25	0.19	0.04	7	3
Autozooeccial wall thickness in endozone	0.005–0.012	0.011	0.002	14	5
Autozooeccial wall thickness in exozone	0.050–0.100	0.066	0.022	8	4

Trematopora sp. can be distinguished from *T. sardoa*, previously described here, because in the former autozooeccial apertures are subcircular, diaphragms can be present in endozone and in exozone and acanthostyles have a smaller diameter. From *T. vesiculata* can be distinguished, besides the presence of vesicular tissue in the new species, because *Trematopora* sp. has smaller acanthostyles (a diameter range of 0.025–0.050 mm in *Trematopora* sp. vs 0.050–0.125 mm in *T. vesiculata*). *Trematopora* sp. is similar to *Trematopora* sp. 1 described by Ernst & Key (2007) in the Upper Ordovician of the Montagne Noire (France), but they can be distinguished because in French species diaphragms are more abundant in exozone and acanthostyles develop from the base of the exozone.

Occurrence. – *Trematopora* sp. is exclusive from the Khabt-el-Hajar Formation in the horizon MS1, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Suborder Esthonioporina Astrova, 1978
Family Aisenvergiidae Dunaeva, 1964

Genus *Eridotrypa* Ulrich, 1893

Type species. – *Cladopora aedilis* Eichwald, 1855 (= *Eridotrypa mutabilis* Ulrich, 1893). Middle Ordovician of Estonia.

Diagnosis. – Following Ernst & Key (2007) *Eridotrypa* is characterized by having ramose colonies with narrow exozone; autozooeccia weakly bending towards zoarial surface, with oval to oval-rounded apertures and arranged in diagonal rows; autozooeccial walls thick and with obliquely laminated microstructure in exozone; autozooeccial diaphragms present in endozone and exozone; mesozooecia rare, short, differently closed at colony surface; acanthostyles scarce, small and short when present.

Occurrence. – This genus range from Lower Ordovician to Middle Devonian and has a wide geographical distribution (North America, North Africa, Europe, Siberian, and Asian).

?Eridotrypa sp.

Figure 7F, Table 15

Material. – MPZ 2014/557–562.

Remarks. – The description of this species is based exclusively on the study of longitudinal sections, so autozooeccial diameters are apparent and the relationship between endozone and exozone is qualitative and not quantitative.

Description. – Ramose colony with narrow exozone. Autozooeccial apertures 0.19 mm of average diameter; throughout endozone autozooeccia are long tubes growing parallel to branch axis, in internal exozone they bend slightly, intersecting zoarial surface with an average angle of 26.5°; diaphragms present throughout autozooeccial tube, scarce in endozone, separated by more than two autozooeccial diameters, and more numerous in exozone, separated approximately by one and half autozooeccial diameters, always thin and perpendicular to walls; autozooeccial walls with microgranular microstructure in endozone, thin (0.011 mm of average thickness) and straight; from internal exozone they progressively thicken until reaching an average thickness of 0.066 mm in zoarial surface, here with obliquely laminated microstructure and a dark thick line separating autozooeccial walls. Mesozooecia and acanthostyles not observed.

Remarks. – The features described in these Moroccan longitudinal sections fit well with the diagnosis of the genus *Eridotrypa* since they share the ramose zoaria with poorly developed exozone, the autozooeccia intersecting zoarial surface at a low angle, the autozooeccial walls thick and with obliquely laminated microstructure in exozone; the presence of autozooeccial diaphragms in endozone and exozone, and, in this case, the absence of mesozooecia and acanthostyles, but neither tangential nor transverse sections have been studied and nothing is known about the shape of autozooeccial apertures and its arrangement in zoarial surface. So, we cannot be completely sure that this material belongs to *Eridotrypa*.

Occurrence. – *?Eridotrypa* sp. is known exclusively from the Khabt-el-Hajar Formation, horizons MN4 and MS5, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Suborder Halloporina Astrova, 1965
Family Halloporidae Bassler, 1911

Genus *Parvohallopora* Singh, 1979

Type species. – *Monticulipora ramosa* d'Orbigny, 1850. Lower Silurian of Cincinnati (Ohio, USA).

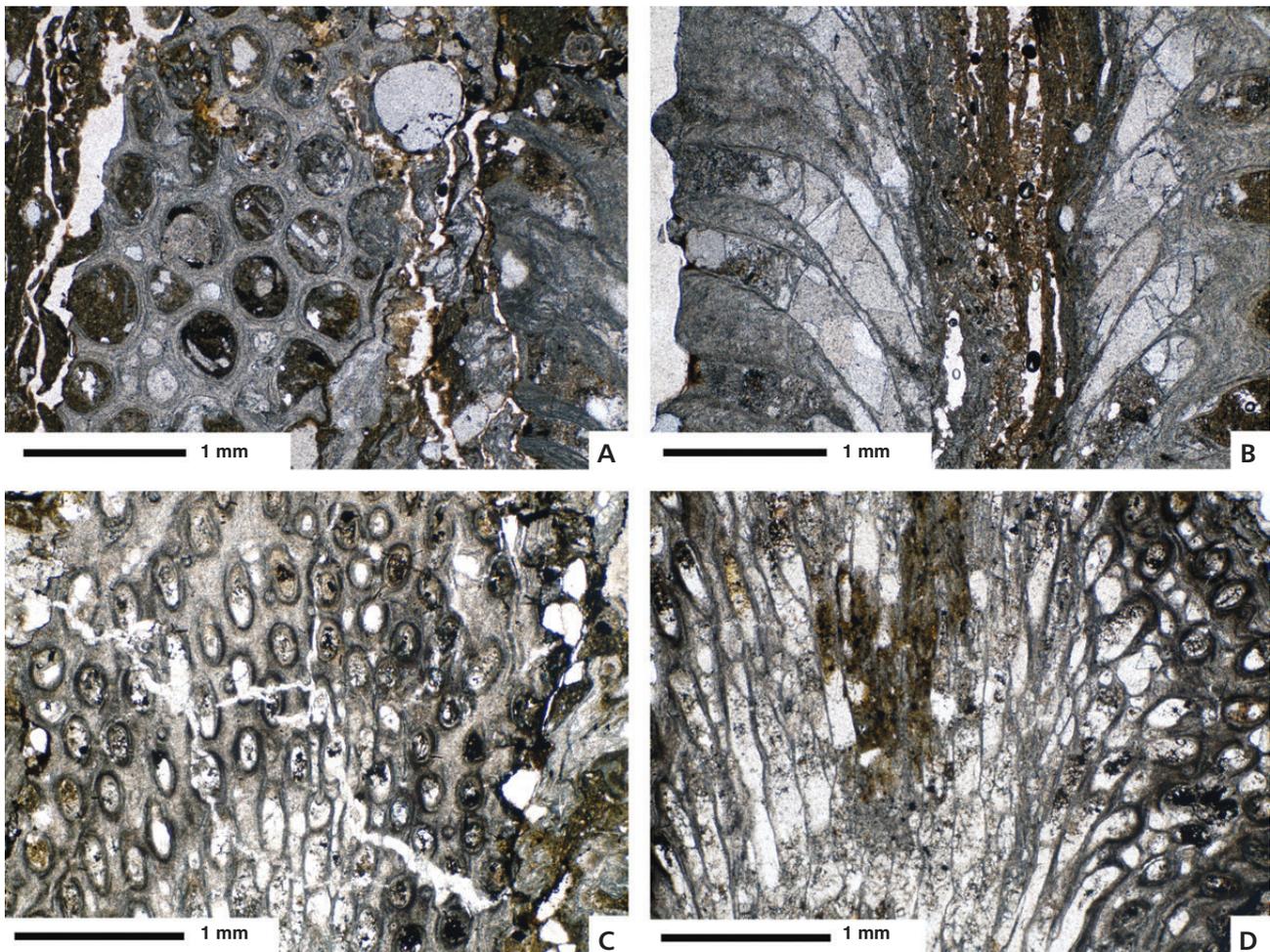


Figure 8. A, B – *Parvohallopora* sp. 1; A – tangential section of specimen MPZ 2014/548; B – longitudinal section of specimen MPZ 2014/547. • C, D – Trepostomate sp. indet., inclined sections of specimen MPZ 2014/572. All specimens from horizon MN4.

Diagnosis. – Following Singh (1979) *Parvohallopora* is characterized by having a ramose zoarium with smooth surface or monticules regularly spaced. Exozone well developed with autozoecia forming sharp angles with zoarial external surface. Autozoecial cross-section irregularly polygonal in endozone and polygonal or circular to subcircular in exozone. Autozoecial diaphragms perpendicular to the autozoecial walls or curved, but rarely cystoidal, present throughout autozoecial tube, although they can be absent in exozone in some species. Mesozoecia present and numerous, circular to subcircular in cross-section and with a diameter less than half of those of autozoecia. Mesozoecial diaphragms numerous, perpendicular to mesozoecial walls or curved. Zoecial walls laminated with an inverse U or V pattern.

Occurrence. – Middle-Upper Ordovician and Lower Silurian of North America, Upper Ordovician of South America and North Africa (Morocco), Upper Ordovician and Lower Silurian of Europe and Mongolia.

***Parvohallopora* sp. 1**

Figure 8A, B, Table 16

Material. – MPZ 2014/547–550.

Description. – Zoaria ramose, but with unknown branch diameter because most part of endozone is destroyed and cross-sections are deformed. Autozoecial cross-sections circular to subcircular in exozone, with an average diameter of 0.29 mm and an average density of 4.2 apertures/mm²; autozoecia curving gently in external endozone and sharply bending in internal exozone, forming an average angle of 75° with zoarial surface; autozoecial diaphragms absent in endozone, scarce in internal exozone and numerous in external exozone, separated by a distance less than 1/2 autozoecial diameter; they are mainly perpendicular to autozoecial walls, but inclined, sinusoidal and even cystoidal shapes are also present; two types of autozoecial diaphragms can be distinguished: the first and most abundant are thin with granular microstructure and

Table 16. Summary of the statistical analysis of *Parvohallopora* sp. 1. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial angle with zoarial surface	57.9–88.0	74.8	9.8	15	4
Autozooeccial diameter	0.22–0.37	0.29	0.03	26	5
Autozooeccia/mm ²	3.0–5.5	4.2	1.8	2	1
Mesozooeccial diameter	0.06–0.17	0.11	0.03	27	5
Mesozooeccial diaphragms/mm	8–18	14	2	18	5
Mesozooeccia/mm ²	3.0–6.0	4.5	2.1	2	1
Zooeccial wall thickness in exozone	0.037–0.150	0.082	0.028	14	3

Table 17. Summary of the statistical analysis of *Trepostomate* sp. indet. Abbreviations as in Table 1.

Character	Or	X	SD	Nm	Nsp
Autozooeccial maximum diameter	0.15–0.25	0.20	0.03	20	2
Autozooeccial minimum diameter	0.09–0.17	0.12	0.02	20	2
Autozooeccial spacing along branch	0.30–0.55	0.37	0.07	12	2
Autozooeccial wall thickness	0.020–0.037	0.027	0.006	16	2
Mesozooeccial diameter	0.037–0.062	0.052	0.009	7	1

terminate in autozooeccial walls; diaphragms of the second type are thick, with laminated microstructure originating from the cortex of autozooeccial walls. Mesozooeccial cross-sections subcircular to subpolygonal in exozone, with an average diameter of 0.11 mm and an average density of 4.5 mesozooeccia/mm²; they develop in external endozone and are densely tabulate by diaphragms with an average of 14 diaphragms/mm; diaphragms mainly perpendicular to mesozooeccial walls, but thick and laminated cystoidal diaphragms also present, originating from the cortex of wall lamination. Zooeccial walls thick in exozone with an average thickness of 0.082 mm and with a clear laminated microstructure showing an inverse V pattern.

Remarks. – The sharp angle formed by autozooeccia and zoarial external surface, the circular to subcircular shape of autozooeccial apertures, the presence of autozooeccial diaphragms in exozone, the large number of mesozooeccia densely tabulate by diaphragms, as well as the zooeccial laminated walls with an inverse V pattern have allow us to assign these specimens to the genus *Parvohallopora*. However we have not found a known *Parvohallopora* species in which this material can be included. It is probably a new species, but we do not have any transversal section and in the longitudinal section most part of the endozone is destroyed, so these characters are unknown. This fact prevents us from defining a new *Parvohallopora* species and opted instead to leave this material in open nomenclature to the species level.

In the Khabt-el-Hajar Formation (Upper Ordovician of Morocco) *P. cystata* Jiménez-Sánchez (in Jiménez-Sánchez *et al.* 2015b) and *Parvohallopora* sp. (Jiménez-Sánchez *et al.* 2015b) have been previously described. The new specimens included in *Parvohallopora* can be distinguished from *P. cystata* because cystoidal diaphragms are abundant in the latter species and it has larger autozooeccial diameter (0.20–0.46 mm in *P. cystata* vs 0.22–0.37 mm in *Parvohallopora* sp. 1 described here). From *Parvohallopora* sp. described in Jiménez-Sánchez *et al.* (2015b) this new material can be distinguished because it has less mesozooeccia/mm² (4.5/mm² in *Parvohallopora* sp. 1 vs 11.0/mm² in *Parvohallopora* sp.), more mesozooeccial diaphragms (14/mm in *Parvohallopora* sp. 1 vs 10/mm in *Parvohallopora* sp.) and by the absence of megazooeccia in *Parvohallopora* sp. 1.

Occurrence. – *Parvohallopora* sp. 1 is exclusive from the Khabt-el-Hajar Formation in the horizons MN4 and MS1, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Incertae sedis

Trepostomate sp. indet.

Figure 8C, D, Table 17

Material. – MPZ 2014/572–573.

Description. – Ramose zoaria with individual branches 4.0 and 4.7 mm in diameter. Autozooeccial cross-section oval in exozone, with an average minimum and maximum diameters of 0.12 mm and 0.20 mm, respectively, and arranged in irregular longitudinal rows; longitudinally spaced 0.37 mm on average; in endozone autozooeccia are long tubes growing almost parallel to branch axis, in internal exozone they strongly bend intersecting zoarial surface with a sharp angle, close to 90°. Autozooeccial diaphragms absent in both endozone and exozone. Autozooeccial walls thin and slightly wavy in endozone, with microgranular microstructure; in internal exozone they progressively thicken until reaching in external exozone an average thickness of 0.027 mm, with a laminated microstructure. Autozooeccial apertures separated by a thick calcitic laminated skeleton, showing some small regular rounded vesicles (0.052 mm of average diameter) in its base.

Remarks. – The zoaria described here have tangential section very similar to that of the cryptostome genus *Oanduelina* Pushkin, 1977, since both have oval autozooeccial apertures arranged in longitudinal rows, vesicles in the endozone-exozone transition covered by extrazooeccial skeleton and exilazooeccia are absent. However, in longitudinal

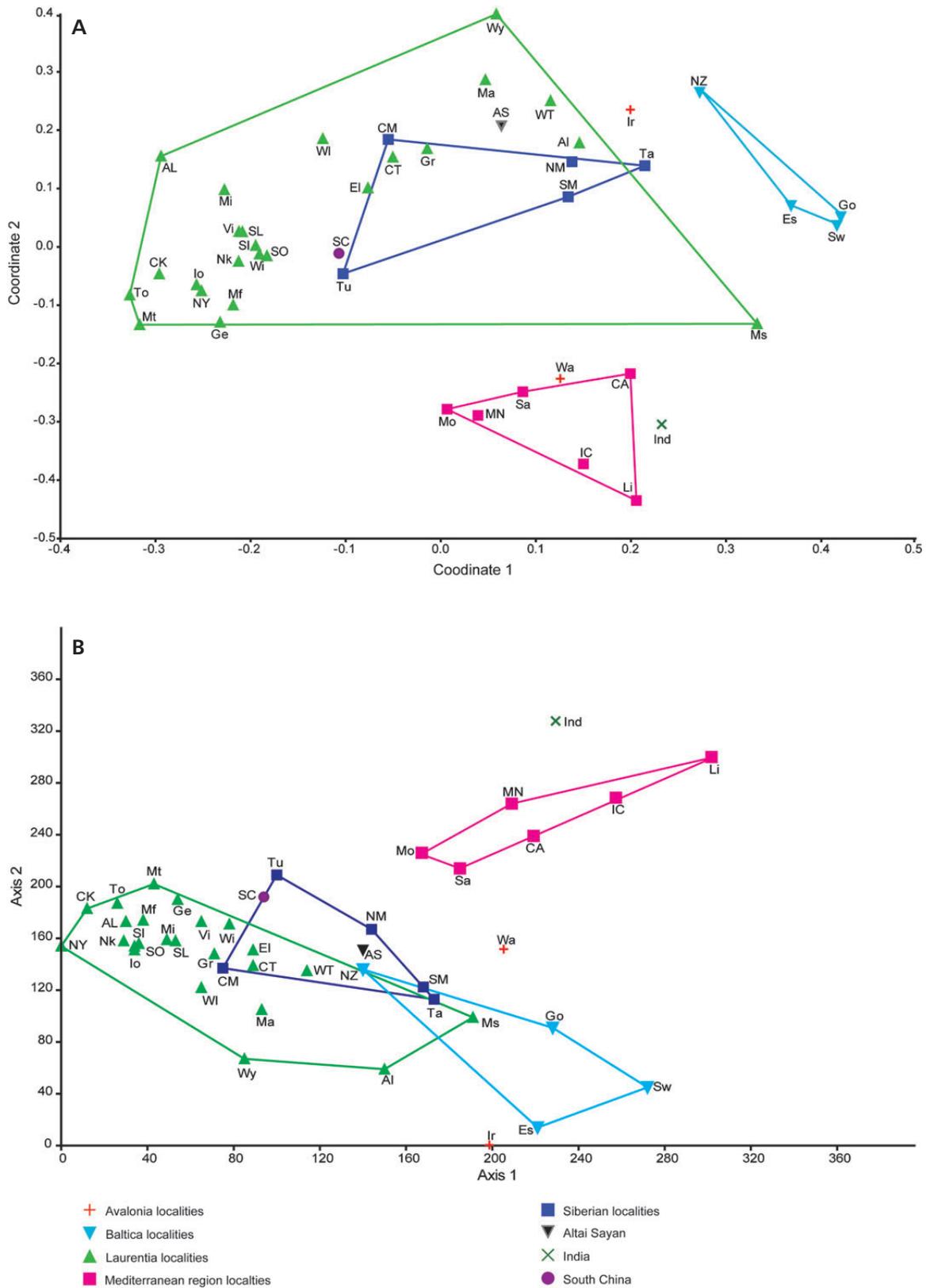


Figure 9. A – principal coordinate analysis (PCO) using the Dice similarity coefficient; the percentage of total variation contained in each coordinate is: axis 1 = 14.22% and axis 2 = 11.25%. • B – detrended correspondence analysis (DCA). See Jiménez-Sánchez & Villas (2010) fig. 1 and table 1 for abbreviations.

section these Moroccan zoaria show long autozoecial tubes, difficult to explain in ptilodictyinae genera and easier to fit in trepostomate ones. This is why we have decided to include this material in the Order Trepostomata, in spite of the similarity to the genus *Oanduellina* in tangential section.

Occurrence. – Trepostomate sp. indet. is known exclusively from the Khabt-el-Hajar Formation, horizon MN4, eastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

Palaeogeography affinities of Moroccan bryozoa

Jiménez-Sánchez & Villas (2010) carried out a complete Upper Ordovician palaeogeography study based on the distribution of upper Katian bryozoan genera. This work was specially focused on the high and middle-high latitude bryozoans from the Mediterranean region (Carnic Alps, Iberian Chains, Libya, Montagne Noire, Morocco and Sardinia), comparing their palaeogeographic affinities with those of other Gondwana areas (India and Argentinian Precordillera) and also with the other Late Ordovician palaeocontinents (Avalonia, Baltica, Laurentia and Siberia) and South China, located in that period in low and middle-low latitudes. They improved the database of Tuckey (1990) for the upper Katian bryozoans and studied the presence/absence of the 136 known genera in 45 localities from all palaeocontinents (Jiménez-Sánchez & Villas 2010, fig. 1). This database was analysed for patterns with two multivariate statistical techniques: detrended correspondence analysis (DCA) and principal coordinate analysis (PCO) (Jiménez-Sánchez & Villas 2010, figs 2–4). For the multivariate analysis to be reliable, only localities with more than 8 identified genera were used. All 45 localities fulfil this constraint except Libya, which only has 7 genera, and Morocco, with 5 genera. They were included in the analysis in order to have a wider view of the palaeogeography of the Mediterranean region. In general terms, the Jiménez-Sánchez & Villas's (2010) analysis clearly separates these 45 localities according to the palaeocontinent they belong to for the Mediterranean region and Baltica (defining the Baltic and Mediterranean provinces, respectively), but not for Laurentia and Siberia, which plot together forming a single Laurentian-Siberian province, and the two localities of Avalonia, whose position depends on the type of multivariate analysis (DCA or PCO).

In more detail, the localities that form each province (Baltica, Mediterranean region and Laurentia-Siberia) are not at the same distance from the centre of their polygon, and some localities systematically plot far from the centre in one or both of the plots (DCA and PCO). This is the case

of Norway in the Baltic province, which plots inside or very close to the point cloud formed by the Mediterranean province localities, and of Missouri in the Laurentian-Siberian province, which plots near the localities of the Baltic province and quite far from the other Laurentian-Siberian localities, both cases in PCO analysis. Also, Morocco and Libya plot quite far from the other Mediterranean localities. Jiménez-Sánchez & Villas (2010) explained these anomalies as a consequence of the low number of identified genera in the case of Morocco, Libya and Norway (with five, seven and eight known genera, respectively) and by the inclusion of possible Hirnantian fauna coming from the Girardeau Limestone in the case of Missouri.

Ernst & Nakrem (2011) studied the bryozoans from the Mjosa Formation (Upper Ordovician of Oslo Region), specifically those of the Bergevik member, considered to be of lower Katian age (Bergström *et al.* 2011). They identified eight genera that were added to the Jiménez-Sánchez & Villas' (2010) upper Katian database. But, although the results slightly improve those of Jiménez-Sánchez & Villas (2010), since Norway plots farther away from the Mediterranean group in the PCA and Novaya Zemlya (NZ) place outside of the polygon defined by the Laurentian-Siberian localities in the DCA, we consider not correct to mixing the lower Katian genera from the Mjosa Formation with the upper Katian genera that form the database of Jiménez-Sánchez & Villas (2010).

Since the palaeogeographic study performed by Jiménez-Sánchez & Villas (2010), important advances in the knowledge of the upper Katian bryozoans from Moroccan have been made. Jiménez-Sánchez *et al.* (2015a, b) described 12 genera in the marly facies of the Khabt-el-Hajar Formation, and in the present work other 13 genera are described, ten of them only identified in the calcarenite facies of this formation. These genera have been added to the database of Jiménez-Sánchez & Villas (2010) making a grand total of 23 genera for Morocco. The updated database has been analysed with the same multivariate techniques employed by Jiménez-Sánchez & Villas (2010) in order to reassess the palaeogeographic affinity of the Moroccan bryozoans, as only five genera were used in the first analysis. The new results show that Morocco bryozoans, in spite of being the fauna developed in the highest latitudes during the upper Katian, have a clear Mediterranean affinity (Fig. 9). Also, the position of Morocco has improved with respect to the other Mediterranean localities, and now plots closer to the rest, although it is still in one of the vertices of the polygon. This position can be a consequence of the high latitude in which the fauna developed.

The palaeogeographic position of Norway during the upper Katian make difficult to explain its faunistic affinity with the Mediterranean region. On the other hand, the only documented genera of this locality are from the Hirnantian (Brood 1980) and from the lower Katian (Ernst & Nakrem

2011), since Tuckey (1990) does not give references of the Norwegian bryozoans included in his database. So, we have removed Norway from the database in this new analysis.

Acknowledgements

We would like to acknowledge the financial support to the project EXLIZ CZ.1.07/2.3.00/30.0013, co-financed by the European Social Fund and the state budget of the Czech Republic, as well as to the project CGL2012-39471 of the Spanish Ministry of Economy and Competitiveness. It is also a contribution to the project E-17 “Heritage and Paleontological Museum”, from the Department of Science, Technology and University of the Government of Aragón, with participation of the European Social Fund, and the IGCP 591 project “ The Early to Middle Paleozoic Revolution”. We also thank the technician support to the Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza. Thanks also to Zarela Herrera and Pierre Clement for field assistance.

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