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

ANDREA JIMÉNEZ-SÁNCHEZ, ANDREJ ERNST, EMMANUELLE VENNIN & ENRIQUE VILLAS

A new study of the Upper Ordovician bryozoans belonging to the families Aisenvergiidae, Amplexoporidae, Arthrostylidae, Enalloporidae, Halloporidae, Heterotrypidae, Mesotrypidae, Pilodictyidae, 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 Fenestra 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.


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 Nicoletella 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 diversity 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).

DOI 10.3140/bull.geosci.1569
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 autozooecial 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 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).](image-url)
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 bidirectional 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
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 devoid 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.

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.

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

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). Cara-doc (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 disseipments; 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.


*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 endzone 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 autozooecia 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 autozooecia in endozone and elliptical autozooecia 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 autozooecia 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.
Enallopora lineata

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 both obverse and reverse surface; 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*.

Remarks. – The shape of the colonies with branches dichotomously divided and not linked by either anastomoses or disseipments; 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*.

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

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

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

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. Autozooecial apertures arranged in 6–8 longitudinal rows, separated by prominent longitudinal ridges. Axial region formed by a lineal axis, where autozooecia budding with an angle of 20°–40°. Autozooecial 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 autozooecial rows from eight or more, as was considered by Bassler (1952), to between six and eight. Conti (1990) included *Ulrichostylus radiatus* with twelve autozooecial rows in the genus *Ulrichostylus*. Ernst & Key (2007) considered again 6 to 8 as the diagnostic number of autozooecial longitudinal rows. We follow Ernst & Key’s (2007) diagnosis, but accept the increase in the number of autozooecial 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.


Description. – Zoarium ramose; individual branches sub-polygonal in cross-section with an average diameter of 0.80 mm. Autozooscleral 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 autozoosclera arranged radially around it. Endozone with an average diameter of 0.31 mm, with triangular autozoosclera growing from the central axis with an average angle of 14.7°. In exozozone autozoosclera 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 autozooscleral walls hyaline, continuous from the central axis, with an average thickness of 0.014 mm; in exozozone walls composed of a hyaline layer, sheathed by outer laminated skeleton; autozooscleral distal wall in exozozone 0.049 mm of average thickness.

Remarks. – The arrangement of autozooscleral apertures in longitudinal rows separated by prominent ridges; the presence of the central axis with autozooscleral rows around it; the shape of autozooscleral cross-section both in endozone and exozone; as well as the absence of autozooscleral diaphragms and mesozooecia 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 autozooscleral diaphragms and acanthostyles, as well as a similar number of autozooscleral rows and similar autozooscleral diameter; consequently these specimens are included in *U. radiatus*.

*Ulrichostylus radiatus* is similar to *U. costatus* Lobdell, 1992, but the former species has more autozooscleral longitudinal rows (7–14 in *U. radiatus* described in Morocco vs 7–8 in *U. costatus*) and smaller autozooscleral 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 Formation (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 Ptilodictyiina Zittel, 1880
Family Ptilodictyiidae 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 exozozone autozoosclera form an angle of 80°–90° with mesotheca; pustules abundant in the autozooscleral boundaries, in the exozonal walls and in the extrazooecial skeleton; autozooscleral cross-section elliptical to oval; superior hemisepta common, generally short and blunt and curving proximally; exilazoecia and monticules absent to rare; extrazooscleral skeleton laminate, commonly crinkled forming longitudinal striae between autozoosclera, 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.
2007 *Graptodictya meneghinii* (Vinassa de Regny, 1942). – Ernst & Key, p. 50, pl. 17, fig. 15, pl. 18, figs 1–3.
**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 autozoecia form with mesotheca both in endozone and exozone; the elliptical to oval shape of autozoecial apertures; the short and blunt shape of superior hemisepta; as well as the laminated and crinkled thick extrazoecial skeleton, forming longitudinal striae between autozoecia. 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 autozoecial 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 autozoecia in endozone; the sharp autozoecial 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 extrazoecial 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 autozoecial 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 autozoecia, subrectangular to subhexagonal in endozone and commonly subrectangular...
in exozone, although oval form can be also present; autozooecial 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. Autozooecia 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). Autozooecia 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 autozooecia forming an angle of about 45° with mesotheca, constant up to zoarial surface. Autozooecial 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 autozooecial apertures arranged in longitudinal rows, separated by straight ridges; the trapezoid autozooecial cross-section in endozone as well as the subromboidal to oval shape in exozone; and the absence of diaphragms are characters present 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 autozooecial apertures (0.10–0.14 mm in the Moroccan material and 0.10–0.13 mm in the Estonian one), the subrectangular to oval autozooecial cross-section in exozone and the constant angle formed by autozooecia from the mesotheca up to the zoarial surface. However, maximum autozooecial 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 (Jõvi 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 Rhinidictyidae 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. Autozooecia growth parallel to mesotheca and strongly bend in internal exozone, without diaphragms or hemisepta. Autozooecial aperture rounded to oval with peristomes, arranged in diagonal rows. Interspace between autozooecia 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 autozooecia 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooezial angle with zoarial surface</td>
<td>72.0°–86.0°</td>
<td>78.5°</td>
<td>4.8</td>
<td>13</td>
<td>3</td>
</tr>
<tr>
<td>Autozooezial aperture minimum diameter</td>
<td>0.08–0.15</td>
<td>0.10</td>
<td>0.02</td>
<td>68</td>
<td>9</td>
</tr>
<tr>
<td>Autozooezia/mm²</td>
<td>8.0–15.0</td>
<td>11.2</td>
<td>2.0</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Autozoeezial aperture spacing diagonally</td>
<td>0.20–0.45</td>
<td>0.32</td>
<td>0.06</td>
<td>24</td>
<td>5</td>
</tr>
<tr>
<td>Autozooezial wall thickness in exozone</td>
<td>0.012–0.050</td>
<td>0.026</td>
<td>0.009</td>
<td>33</td>
<td>8</td>
</tr>
<tr>
<td>Extrazoeezial skeleton thickness</td>
<td>0.19–0.35</td>
<td>0.26</td>
<td>0.05</td>
<td>17</td>
<td>4</td>
</tr>
<tr>
<td>Number of autozoeezial rows in 5 mm diagonally measured</td>
<td>14–18</td>
<td>16</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Stellathostyles diameter</td>
<td>0.025–0.100</td>
<td>0.053</td>
<td>0.015</td>
<td>31</td>
<td>7</td>
</tr>
<tr>
<td>Stellathostyles/mm²</td>
<td>4–13</td>
<td>9</td>
<td>3</td>
<td>9</td>
<td>4</td>
</tr>
</tbody>
</table>

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

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

**Material.** – MPZ 2014/537–545.

**Description.** – Bifoliate branching colonies with maximum and minimum branch diameter unknown since no transversal section has been obtained. Autozooezial apertures rounded to oval with an average diameter of 0.10 mm and an average of 11.2 autozooezia/mm²; arranged in diagonal rows with an average spacing of 0.32 mm between autozoeezial apertures and 16 rows/5 mm in diagonal direction; autozooezia growing recumbent on mesotheca; at base of exozone they bend sharply forming an average angle of 78.5° with zoarial surface; autozoeezial 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; autozoeezial 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 extrazoeezial skeleton with an average thickness of 0.26 mm. Stellathostyles large (0.053 mm of average diameter) and abundant (9 stellathostyles /mm²) and located in laminated extrazoeezial skeleton; they are composed of a distinct light hyaline lumen with radially arranged rays, surrounded by sheaths. Macula absent.

**Remarks.** – The development of autozoeezia, growing parallel to mesotheca and strongly bend at the base of exozone; the absence of diaphragms and hemisepta; the shape of autozoeezial apertures and its arrangement in the zoarial surface; the presence of vesicular tissue between autozoeezia, 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 Stellatodicyta. These specimens fit well with Stellatodicyta 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 autozoeezial diameter (0.09–0.15 mm in the French material and 0.07–0.15 mm in the Moroccan material) and similar number of autozoeezial 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**

**Ptilodictyne sp. indet.**

**Figure 4F, Table 6**

**Material.** – MPZ 2014/546.

**Description.** – Branch colony apparently bifoliate and with unknown diameter. Autozoeezia forming and initial angle of 24° with mesotheca, then they lightly bend and grow parallel to mesotheca in endozone; in exozone autozoeezia sharply bend forming an average angle of 57° with zoarial surface. Autozoeezial apertures apparently arranged in longitudinal rows, with a spacing of 0.51 mm along branch; autozoeezial cross-section circular with an average diameter of 0.12 mm. Autozoeezial 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 autozoeezial 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.
Remarks. – This specimen can be included in the suborder Ptilodictyina since it has a bifoliate zoarium and short autozooecia 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. Autozooecia budding in 8–12 radial series from the central part of the branch, with 2–4 autozooecial rows per series. Radial autozooecial groups are separated by a layer produced by the thickening of autozooecial walls in neighbouring series. Autozooecial diaphragms rare to absent. Acanthostyles can be present. Exilazooecia present, rounded to polygonal in shape. Maculae not observed.

Radiotrypa sp.
Figure 5A, B, Table 7


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. Autozooecial apertures with an apparent diameter of 0.12 mm on average (measured in longitudinal sections); autozooecial 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 autozooecial rows per series; diaphragms scarce, present in external endozone with no more than one or two per autozooecium. Autozooecial walls laminated, with an average thickness of 0.016 mm in endozone and 0.045 mm in exozone. Laminae separating autozooecial radial series with laminar microstructure, thicker than autozooecial walls in endozone but thinner in exozone. Exilazooecia and acanthostyles absent.

Remarks. – The arrangement of autozooecia in radial series from the central part of the branch, with these series separated by a laminated layer produced by the thickening of autozooecial walls in neighbouring series, together with the scarcity of autozooecial 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 exilazooecia 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 mesozooecia. Autozooecial diaphragms generally scarce in endozone and more abundant in exozone, where they are thin, planar, perpendicular to zooecial walls and regularly spaced; autozooecial walls with variable thickness. Intermonticular mesozooecia range from abundant to absent; commonly develop moniliform chambers at proximal ends and tend to become smaller or are terminated distally within exozone; mesozooecial...
diaphragms thicker and more abundant than autozooecial 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter</td>
<td>0.05–0.10</td>
<td>0.08</td>
<td>0.010</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Acanthostyles/mm²</td>
<td>21–25</td>
<td>22</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelial diameter</td>
<td>0.17–0.29</td>
<td>0.22</td>
<td>0.04</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelial apertures/mm²</td>
<td>9–13</td>
<td>10</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelial wall thickness in endozone</td>
<td>0.007–0.012</td>
<td>0.011</td>
<td>0.002</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelial wall thickness in exozone</td>
<td>0.025–0.050</td>
<td>0.037</td>
<td>0.009</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Branch minimum diameter</td>
<td>2.9</td>
<td>2.9</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Endozone minimum diameter</td>
<td>1.7</td>
<td>1.7</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Exozone thickness</td>
<td>0.67–0.75</td>
<td>0.70</td>
<td>0.05</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Mesozoocelial diameter</td>
<td>0.07–0.12</td>
<td>0.10</td>
<td>0.02</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Mesozoocelial apertures/mm²</td>
<td>17–21</td>
<td>19</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

**Remarks.** – The ramose colony, the presence of autozoocelial diaphragms in endozone and its shape, the mesozoocelial diaphragms thicker and more abundant than autozoocelial diaphragms, the moniliform chambers of mesozoecia, 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 autozoocelial 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 autozoocelial diaphragms, autozoecia 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).

**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; autozoocelial diaphragms scarce, typically absent in endozone and widely sparse or even absent in exozone; zooecial walls crenulated and irregularly thick in exozone; mesozoecia rare or absent in intermonticular area; as well as acanthostyles present in endozone and exozone, placed mainly in zooecial 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 megazoecia forming maculae. Autozoecial cross-section round to irregularly polygonal in exozoec, with an average diameter of 0.26 mm and an average areal density of 9.5 apertures/mm²; diaphragms present only in some autozoecia, but no more than two per autozoecium, placed mainly in the distal part of tubes. Mesozooecia developed in exozoec 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 endozoec and exozoec and placed in autozoecial corners; composed of a central hyaline core and dark sheaths surrounding it. Zoecial walls slightly undulating and with irregular thickness (0.010 mm of average thickness in exozoec and slightly thinner in endozoec).

**Remarks.** – The scarcity of autozoecial diaphragms and its complete absence in mesozooecia; the presence of large acanthostyles in autozoecial corners, both in endozoec and exozoec; and the undulated and irregular thickness of autozoecial 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 autozoecia, mesozooecia and acanthostyles in the colonies; besides, the range of diameters of these structures is similar (for autozoecia 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>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter</td>
<td>0.050–0.10</td>
<td>0.072</td>
<td>0.020</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Acanthostyles/mm²</td>
<td>3.0–4.0</td>
<td>3.5</td>
<td>0.7</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Autozoecial aperture diameter</td>
<td>0.19–0.30</td>
<td>0.26</td>
<td>0.04</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Mesozooecial diameter</td>
<td>0.08–0.15</td>
<td>0.11</td>
<td>0.03</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Autozoecial wall thickness</td>
<td>0.007–0.012</td>
<td>0.010</td>
<td>0.002</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Autozoecial apertures/mm²</td>
<td>9.0–10.0</td>
<td>9.5</td>
<td>0.7</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Mesozooecial apertures/mm²</td>
<td>5.0–6.0</td>
<td>5.5</td>
<td>0.7</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

Moroccan *Dekayia* sp., described by Jiménez-Sánchez et al. (2015b), also in the Khabt-el-Hajar Formation, because *Dekayia* sp. has more regular polygonal autozoecia, fewer mesozooecia (a range of 0.5–3.0/mm² in *Dekayia* sp. vs 5.0–6.0/mm² in *D. minima*), larger autozoecia (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 Ugga 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** Mesotrypoidea 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. Autozoecial apertures polygonal, rounded to oval; autozoecial walls slightly thickened in exozoec, with laminated microstructure; diaphragms more abundant in exozoec than in endozoec, where they can be absent, and cystiphrags only in exozoec. 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.

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozoocelia angle with zoarial surface</td>
<td>35°–66°</td>
<td>46°</td>
<td>14.2</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelia diameter</td>
<td>0.12–0.17</td>
<td>0.15</td>
<td>0.02</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Branch minimum diameter</td>
<td>3.48</td>
<td>3.48</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Endozone wall thickness</td>
<td>0.005–0.012</td>
<td>0.007</td>
<td>0.003</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Exozone wall thickness</td>
<td>0.050–0.100</td>
<td>0.072</td>
<td>0.021</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

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.

Material. – MPZ 2014/553.

Description. – Ramose colony with a branch diameter of 3.5 mm and autozoocelia average diameter of 0.15 mm in exozone (measured in longitudinal section). In endozone autozoocia 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°. Autozoocelia 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 autozoocelia walls (side facing branch axis), and irregular in size within the same autozoocium. Mesozooecia not observed. Acanthostyles scarce, developed inside autozoocelia walls in external exozone. Autozoocelia 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 autozoocelia 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 (France) and it is included in this species. In both materials autozoocia reach zoarial surface with similar angle, diaphragms and cystiphragms have the same distribution and similar shape; endozone and exozone autozoocelia 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 autozoocelia 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 autozoocelia 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

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

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozoocelia angle with zoarial surface</td>
<td>80°–89°</td>
<td>86°</td>
<td>3</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Autozoocelia maximum diameter</td>
<td>0.14–0.25</td>
<td>0.18</td>
<td>0.03</td>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td>Autozoocelia minimum diameter</td>
<td>0.07–0.15</td>
<td>0.11</td>
<td>0.02</td>
<td>25</td>
<td>3</td>
</tr>
<tr>
<td>Autozoocelia cingulum thickness</td>
<td>0.020–0.037</td>
<td>0.027</td>
<td>0.004</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>Autozoocelia wall thickness in endozone</td>
<td>0.006–0.010</td>
<td>0.007</td>
<td>0.002</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Branch minimum diameter</td>
<td>3.8–4.2</td>
<td>4.0</td>
<td>0.3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Endozone minimum diameter</td>
<td>2.85–2.92</td>
<td>2.89</td>
<td>0.05</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Exozone thickness</td>
<td>0.45–0.57</td>
<td>0.52</td>
<td>0.04</td>
<td>6</td>
<td>2</td>
</tr>
</tbody>
</table>
ramose zoarium with long autozoecia growing parallel to the branch axis in endozone and curving in exozone to form an angle of up to 90° with the zoarial surface. Autozoecial cross-section irregularly polygonal in endozone and rounded-polygonal or oval in exozone. Autozoecial diaphragms scarce or absent in endozone and exozone. Autozoecial walls thin in endozone and progressively thicker in exozone, showing a distinct fine lamination. Mesozooecia present, partitioned by both diaphragms and cysts in the same mesozooecium, and sometimes also filled with vesicular tissue; usually mesozooecia 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


**Description.** – Ramose zoaria with individual branches 4.0 mm of average diameter. Autozoecial 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 autozoecia is generally larger than its minimum diameter and this space is occupied by calcitic deposits. Autozoecia irregularly polygonal in endozone; here they grow parallel to branch axis and curve gently in external endozone; at the base of exozone autozoecial curvature becomes stronger, forming an average angle of 86° with zoarial surface. Autozoecial diaphragms only present in some autozoecia, both in endozone and exozone and with a large separation between consecutive diaphragms. Autozoecial walls slightly undulated, thin in endozone (0.007 mm of average thickness) and not distinguishable from the cingulum in exozone. Autozoecial walls become thicker and in zoarial surface mesozooecial apertures are completely cover by calcitic laminated skeleton; acanthostyles abundant, often arranged near peristome or in mesozooecial walls.

**Remarks.** – The ramose zoarial growth habit, with long autozoecia growing parallel to the branch axis in endozone and curving in exozone to form sharply angle with the zoarial surface; the shape of autozoecial cross section both in endozone and exozone, the scarcity of autozoecial diaphragms; and especially the presence of numerous mesozooecia filled with calcitic deposits, that prevent seeing them in the external colonial surface, and the presence of vesicular structures inside these mesozooecia 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*).

**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; autozoecial apertures oval to rounded and with peristome, autozoecial diaphragms scarce and often absent in endozone; mesozooecia numerous and densely tabulated by diaphragms, with thin walls and beaded in internal exozone; near surface mesozooecia filled with calcitic deposits, that prevent seeing them in the external colonial surface, and the presence of vesicular structures inside these mesozooecia 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.

*Trematopora* 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).

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

Figure 6E, F, Table 12

1942 *Leptorypella?* sardoa Vinassa de Regny; Vinassa de Regny, pp. 1039–1040, pl. 3, figs 9–12.


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.
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. Autozoocodial 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 autozoocia/mm² in endozone autozoocia are long tubes growing parallel to branch axis; in internal exozone they strongly bend, forming an average angle of 62° with zoarial surface. Autozoocial 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. Autozoocial diaphragms scarce, straight in shape, and present only in internal exozone. Mesozoocia 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 mesozoocia, 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 autozoocial walls, but without modifying them.

Remarks. – The oval shape of autozoocial apertures; the scarcity of autozoocial diaphragms; the abundance of mesozoocia 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 specimens have been included in this species since they show its diagnostic characters (average size of the colonies and its polymorphs, oval autozoocial apertures, scarcity of autozoocial diaphragms and abundance of mesozoocia).

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 autozoocial apertures and autozoocial 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 synonym 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 autozoocial diaphragms in the endozone and acanthostyles develop from the internal exozone. From T. acanthostylita can be distinguished because in this species the autozoocial 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 horizon and locality. – Merzane North section, horizon 4. Upper Katian (Upper Ordovician) of Morocco.


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

Diagnosis. – Trematopora characterized by the presence of thick vesicular tissue in mesozoocia.
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. Autozooecial cross-section rounded to slightly oval in exozone, with an average diameter of 0.12 mm; in endozone autozooecia are long tubes growing parallel to branch
**Table 13.** Summary of the statistical analysis of *Trematopora vesiculata* sp. nov. Abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>Ort</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter</td>
<td>0.050–0.125</td>
<td>0.076</td>
<td>0.021</td>
<td>19</td>
<td>3</td>
</tr>
<tr>
<td>Autozooidal angle with zoarial</td>
<td>72.0°–86.0°</td>
<td>79.4°</td>
<td>4.3</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>surface</td>
<td>0.10–0.16</td>
<td>0.12</td>
<td>0.02</td>
<td>18</td>
<td>3</td>
</tr>
<tr>
<td>Autozooidal aperture diameter</td>
<td>0.020–0.030</td>
<td>0.025</td>
<td>0.002</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Autozooidal wall thickness</td>
<td>3.8</td>
<td>3.8</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Branch thickness</td>
<td>2.3</td>
<td>2.3</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Endozone diameter</td>
<td>0.75–0.80</td>
<td>0.76</td>
<td>0.02</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Exozone width</td>
<td>0.257–0.450</td>
<td>0.49</td>
<td>0.05</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

**Remarks.** – The rounded shape of autozooidal apertures; the scarcity of autozooidal diaphragms, absent in most autozooidal; the abundance of mesozooecia covered by calcitic deposits in the zoarial surface; the large size of acanthostyles; as well as the microstructures of zooidal 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.

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**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 autozoecia 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 Khabt el-Hajar Formation, horizon MN4, in the northeastern Moroccan Anti-Atlas (Upper Ordovician, upper Katian).

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

<table>
<thead>
<tr>
<th>Character</th>
<th>Ort</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthostyles diameter</td>
<td>0.025–0.05</td>
<td>0.037</td>
<td>0.009</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Autozooidal angle with zoarial</td>
<td>59°–90°</td>
<td>77°</td>
<td>13</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>surface</td>
<td>0.07–0.12</td>
<td>0.10</td>
<td>0.02</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>Autozooidal minimum diameter</td>
<td>0.025–0.040</td>
<td>0.033</td>
<td>0.006</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Autozooidal wall thickness</td>
<td>0.37–0.55</td>
<td>0.49</td>
<td>0.05</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

**Remarks.** – The subcircular shape of autozooidal apertures; the scarcity of autozooidal 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.
Trematopora sp. can be distinguished from T. sardoa, previously described here, because in the former autozooecial 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; autozooecia weakly bending towards zoarial surface, with oval to oval-rounded apertures and arranged in diagonal rows; autozooecial walls thick and with obliquely laminated microstructure in exozone; autozooecial diaphragms present in endozone and exozone; mesozoocoea 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).

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

<table>
<thead>
<tr>
<th>Character</th>
<th>Or</th>
<th>X</th>
<th>SD</th>
<th>Nm</th>
<th>Nsp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autozooecial angle with zoarial surface</td>
<td>18°–36°</td>
<td>26°</td>
<td>6</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Autozooecial diameter</td>
<td>0.15–0.25</td>
<td>0.19</td>
<td>0.04</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Autozooecial wall thickness in endozone</td>
<td>0.005–0.012</td>
<td>0.011</td>
<td>0.002</td>
<td>14</td>
<td>5</td>
</tr>
<tr>
<td>Autozooecial wall thickness in exozone</td>
<td>0.050–0.100</td>
<td>0.066</td>
<td>0.022</td>
<td>8</td>
<td>4</td>
</tr>
</tbody>
</table>

?Eridotrypa sp.
Figure 7F, Table 15


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

Description. – Ramose colony with narrow exozone. Autozooecial apertures 0.19 mm of average diameter; throughout endozone autozooecia 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 autozooecial tube, scarce in endozone, separated by more than two autozooecial diameters, and more numerous in exozone, separated approximately by one and half autozooecial diameters, always thin and perpendicular to walls; autozooecial 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 autozooecial walls. Mesozoocoea 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 autozooecia intersecting zoarial surface at a low angle, the autozooecial walls thick and with obliquely laminated microstructure in exozone; the presence of autozooecial diaphragms in endozone and exozone, and, in this case, the absence of mesozoocoea and acanthostyles, but neither tangential nor transverse sections have been studied and nothing is known about the shape of autozooecial 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).
Diagnosis. – Following Singh (1979), *Parvohallopora* is characterized by having a ramose zoarium with a smooth surface or monticules regularly spaced. Exozone well developed with autozooecia forming sharp angles with zoarial external surface. Autozoocelial cross-section irregularly polygonal in endozone and polygonal or circular to subcircular in exozone. Autozoocelial diaphragms perpendicular to the autozoocelial walls or curved, but rarely cystoidal, present throughout autozoocelial tube, although they can be absent in exozone in some species. Mesozooecia present and numerous, circular to subcircular in cross-section and with a diameter less than half of those of autozooecia. Mesozooecial diaphragms numerous, perpendicular to mesozooecial walls or curved. Zoocelial 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


Description. – Zoaria ramose, but with unknown branch diameter because most part of endozone is destroyed and cross-sections are deformed. Autozoocelial cross-sections circular to subcircular in exozone, with an average diameter of 0.29 mm and an average density of 4.2 apertures/mm²; autozoocelia curving gently in external endozone and sharply bending in internal exozone, forming an average angle of 75° with zoarial surface; autozoocelial diaphragms absent in endozone, scarce in internal exozone and numerous in external exozone, separated by a distance less than 1/2 autozoocelial diameter; they are mainly perpendicular to autozoocelial walls, but inclined, sinusoidal and even cystoidal shapes are also present; two types of autozoocelial diaphragms can be distinguished: the first and most abundant are thin with granular microstructure and...
terminate in autozooecial walls; diaphragms of the second type are thick, with laminated microstructure originating from the cortex of autozooecial walls. Mesozooecial cross-sections subcircular to subpolygonal in exozone, with an average diameter of 0.11 mm and an average density of 4.5 mesozooecia/mm²; they develop in external endozone and are densely tabulate by diaphragms with an average of 14 diaphragms/mm; diaphragms mainly perpendicular to mesozooecial walls, but thick and laminated cystoidal diaphragms also present, originating from the cortex of wall lamination. Zoecial 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 autozooecia and zoarial external surface, the circular to subcircular shape of autozooecial apertures, the presence of autozooecial diaphragms in exozone, the large number of mesozooecia densely tabulate by diaphragms, as well as the zoecial 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 autozooecial 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 mesozooecia/mm² (4.5/mm² in Parvohallopora sp. 1 vs 11.0/mm² in Parvohallopora sp.), more mesozooecial diaphragms (14/mm in Parvohallopora sp. 1 vs 10/mm in Parvohallopora sp.) and by the absence of megazooecia 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

Trepostomatae indet.

Figure 8C, D, Table 17


Description. – Ramose zoaria with individual branches 4.0 and 4.7 mm in diameter. Autozooecial 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 autozooecia 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°. Autozooecial diaphragms absent in both endozone and exozone. Autozooecial 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. Autozooecial 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 autozooecial apertures arranged in longitudinal rows, vesicles in the endozone-exozone transition covered by extrazooecial skeleton and exilazooecia are absent. However, in longitudinal...
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.

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 autozooecial 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 Precordilleran) 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 Bergevika 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 Morocco 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 Aragon, 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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