

# Ordovician sponges from the Lenoir Limestone, Tennessee: new evidence for a differential sponge distribution along the margins of Laurentia

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**Abstract.**—Five genera of anthaspidellid and streptosollenid demosponges are described from the Ordovician Lenoir Limestone near Lenoir City, Loudon County, Tennessee, USA including: *Rhopalocoelia regularis* Raymond and Okulitch, *Rugocoelia loudonensis* n. sp., *Psarodictyum* sp. (Anthaspidellidae), *Allosacus pedunculatus* n. sp., and *Zitebella varians* Raymond and Okulitch (Streptosolenidae). These findings confirm the major paleobiogeographic picture for Laurentian sponges (i.e., the differential distribution of sponge faunas along both North American margins), because none of these eastern margin species has been reported from western margin faunas. Only one genus typical of the Great Basin fauna, *Rugocoelia* Johns, 1994, is reported from Tennessee, but as a new species. Possible explanations are discussed for this differential distribution, mainly related to climatic constraints or sedimentary differences, preventing the free distribution of sponge species between Laurentian continental margins.

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## Introduction

Fossil sponges are a well-known faunal component of the Upper Ordovician (Sandbian) Lenoir Limestone (lower Chickamauga Group) of the Valley and Ridge Provenance of east Tennessee, USA. Although mentioned in several papers dealing with lower Paleozoic sponges (Raymond and Okulitch, 1940; Finks and Rigby, 2004) and stratigraphy (Benedict and Walker, 1978; Walker and Benedict, 1980; Shanmugam and Walker, 1983), the fossil sponge fauna from the Ordovician Lenoir Limestone of East Tennessee was never studied in detail (Myers et al., 2009).

Occurrences of sponges in the Lenoir Limestone and other localities in eastern North America were among the first Ordovician fossil sponge localities to be described from the continent, including the Trenton Limestone at Dixon, Illinois (Ulrich and Everett, 1890), Mingan Island, Quebec, Canada, and Valcour Island, New York (Raymond and Okulitch, 1940, later revised by Rigby and Desrochers, 1995). Sponges from western North America were first described from the Pogonip Group in Nevada (Bassler, 1941).

Raymond and Okulitch (1940) investigated Lower to Middle Ordovician sponges from the Mingan Islands of the Champlain Valley, Tennessee and Virginia. From Tennessee, they mentioned *Hudsonospongia cyclostoma* Raymond and Okulitch, 1940 (Lenoir Limestone, Knoxville, Tennessee), *Rhopalocoelia regularis* Raymond and Okulitch, 1940 (Sevier Shale near Neubert, Tennessee), *Allosacus* sp. (Ottosee and

Lenoir Limestone), and *Zitebella pannosa* Raymond and Okulitch, 1940 (Ottosee Limestone).

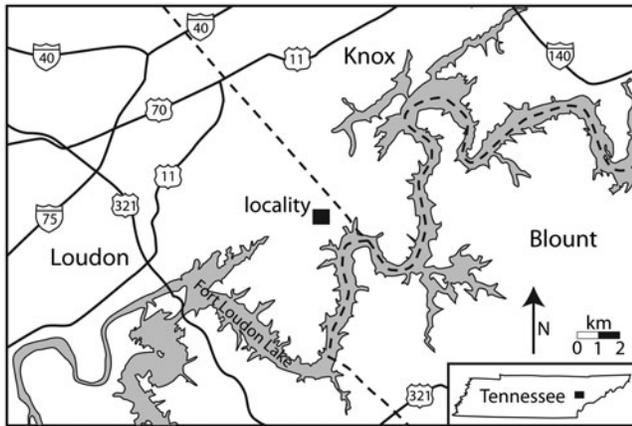
The aim of this contribution is to describe the diverse sponge fauna collected from the Lenoir Limestone, east of Lenoir City, Loudon County, Tennessee. Furthermore, we will discuss the paleobiogeographical implications of this association in the context of the North American sponge distribution.

## Geology and stratigraphy

In the study area, the middle and lower parts of the Chickamauga Group are a thick (~450 m) succession of limestones and shales in the Valley and Ridge provenance of East Tennessee (Fig. 1). The unit thickens and becomes more clastic to the southeast. The base of the Lenoir Limestone suggests restricted peritidal deposition with cryptagal laminated micrites, and a sparse fauna including large leperditid ostracodes and gastropods (Walker and Benedict, 1980). The upper part of the unit shows deeper subtidal environments and becomes more open marine with a rich and diverse fauna. Regionally, the Lenoir Limestone overlies and interfingers with the Athens Formation and is overlain by the Holston Limestone.

The sponge fauna described here was collected from the Upper Ordovician (Middle Ordovician in older literature) Lenoir Limestone, which is a gray, nodular, argillaceous limestone with minor interbedded shale. Limestones range from bioclastic wackestones to packstones and bear an open marine fauna. The fauna is dominated by large complete to fragmented sponges, pelmatozoan ossicles, trilobite sclerites, brachiopods, gastropods and bryozoans. The presence of large digitate crinoid holdfasts suggests that some areas had a soft to firm bottom.

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**Figure 1.** Geographic map and location of the collecting locality east of Lenoir City, Loudon County, Tennessee.

Sponges were collected from the edge of a small sinkhole from a heavily weathered exposure of the Lenoir sponge beds. Sponges were seen both weathering free from matrix and incorporated into limestone slabs ranging from a few to tens of cm thick. The slabs ranged from wakestones to bioclastic grainstones dominated by echinoderm ossicles. Some of the beds were lightly bioturbated with grain filled and mud filled burrows.

Sponge specimens included mostly free and toppled specimens in the rock matrix. More fragile forms were often somewhat compressed and fragmented with spongocoels filled with matrix. The toppled and fragmented nature of some of the sponges suggests that they were subjected to high energy associated with storm events. No clear evidence was seen locally of in place bioherms of other organic buildups.

## Materials

*Repository and institutional abbreviation.*—The specimens are housed under the prefix MMNHC in the McClung Museum of Natural History and Culture (MMNHC) at the University of Tennessee.

## Systematic paleontology

Class Demospongea Sollas, 1875  
 Order Orchocladina Rauff, 1895  
 Family Anthaspidellidae Ulrich in Miller, 1889  
 Genus *Rugocoelia* Johns, 1994

*Type species.*—*Rugocoelia eaganensis* Johns, 1994.

*Rugocoelia loudonensis* new species  
 Figure 2.1–2.7

*Type specimens.*—Holotype MMNHC 13274, and eight paratypes MMNHC 13275–13282 from the Lenoir Limestone East of Lenoir City, Loudon Co., Tennessee, Upper Ordovician (Sandbian).

*Diagnosis.*—*Rugocoelia* with thin walls, 7 mm on average, and wide central cavity. Surface marked by regular circumferential

ripple-like ridges 1–2 mm high, 1–1.5 mm across, and a spacing of 3–5 mm between ridge crests. Radial canals vertically stacked, separated by parietal distances of 0.4–1.1 mm. Canals straight, ~0.2–0.7 mm in diameter. Anthaspidellid skeleton, with two trabs between radial canals in tangential section, and commonly two or three parietal trabs in transverse section.

*Occurrence.*—Lenoir Limestone (Upper Ordovician) East of Lenoir City, Loudon, Co., Tennessee.

*Description.*—Lamellate, open conical or bowl-shaped sponge sometimes slightly pedunculated, with overall height reaching 70 mm. The maximum diameter occurs at the top of the sponge reaching 60 mm. Relatively thin walls, 7 mm on average, outlining a wide open central cavity that reaches almost to the base of the sponge body. Surface marked by regular circumferential ripple-like ridges 1–2 mm high, 1–1.5 mm across and a spacing of 3–5 mm between ridge crests.

Radial canals vertically stacked, separated by parietal distances of 0.4–1.1 mm. Canals straight, ~0.2–0.7 mm in diameter. Rare vertical canals occur in transverse section, 0.2 mm in diameter.

Scalariform anthaspidellid skeletal net, regularly with two trabs between radial canals in tangential section, and commonly two or three parietal trabs in transverse section. The longitudinal section also shows main columnar trabs separating pores and thin regularly intercalated intraparietal trabs. Surface of trab divergence along and parallel to gastral margin.

Amphiarborescent monoclones dominate, but polyclonid and Y-shaped dendroclones are also common in endosomal parietal walls. Endosomal spicules 0.35–0.7 mm long.

Ectosomal dermal layer not well preserved. Dermal pores usually 0.4–0.9 mm across, generally spaced 0.4–0.9 mm apart in both vertical and parietal directions. Spiculation and pore pattern of ectosome reflects that of underlying endosome.

*Etymology.*—*Rugocoelia loudonensis*: from Loudon Co., Tennessee.

*Remarks.*—The Tennessee material is, in many respects, similar to the type species *Rugocoelia eaganensis* Johns, 1994 from the Lower Ordovician, Egan Range, Nevada. However, the wall of our material is considerably thicker and the diagnostic ridges are more tightly spaced than the type species.

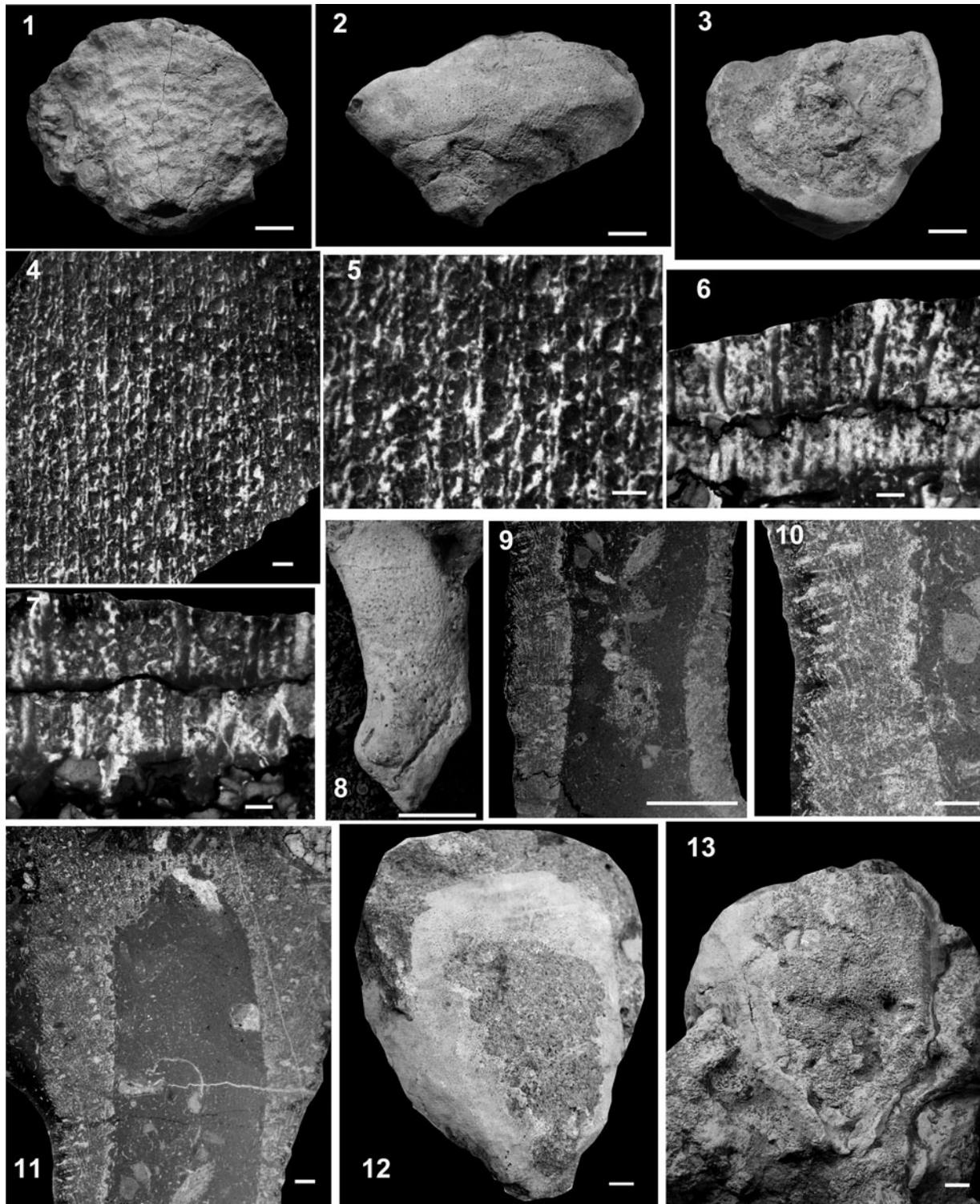
Genus *Rhopalocoelia* Raymond and Okulitch, 1940

*Type species.*—*Rhopalocoelia clarkii* Raymond and Okulitch, 1940.

*Rhopalocoelia regularis* Raymond and Okulitch, 1940  
 Figure 2.8–2.11

*Type specimen.*—Holotype, Museum of Comparative Zoology 9332, Sevier Formation (Upper Ordovician) east Knoxville, Tennessee.

*Occurrence.*—Lenoir Limestone (Upper Ordovician) east of Lenoir City, Loudon, Co., Tennessee. The type species was



**Figure 2.** (1–7) *Rugocoelia loudonensis* n. sp. (1) Lateral view showing the concentric, regularly spaced ridges and the basal view of the deep central cavity, holotype MMNHC 13274, scale bar 10 mm; (2) lateral view of a complete specimen, MMNHC 13275, scale bar 10 mm; (3) dorsal view of a complete specimen showing the open, broad spongocoel and thin walls, MMNHC 13276, scale bar 10 mm; (4) detail of the spicular net in longitudinal view, showing typical anthaspidellid organization, MMNHC 13277, scale bar 1 mm; (5) detail of the previous photograph, showing regular anthaspidellid skeleton with main columnar trabs separating rounded pores and thin regularly intercalated intraparietal trabs, scale bar 1 mm; (6) transverse thin section showing straight canals passing through the entire wall, MMNHC 13278, scale bar 1 mm; (7) transversal thin section showing a different sector of the wall with better-defined intraparietal spicules between canals, scale bar 1 mm. (8–11) *Rhopalocoelia regularis* Raymond and Okulitch. (8) Lateral view of an almost complete specimen with smooth external surface, MMNHC 13263, scale bar 10 mm; (9) longitudinal thin section of the same specimen figured in (8), showing thick walls and deep spongocoel and the typical anthaspidellid scalariform skeleton with mid wall trab divergence, scale bar 5 mm; (10) detail of (9) showing a closer view of the spicular net of vertically bending trabs and transversal radial canals, some of them expanded at mid wall or near the gastral cavity, scale bar 1 mm; (11) almost complete longitudinal section showing the expansion of sponge diameter, a part of the tangential view of the skeleton showing rounded pores, scale bar 1 mm. (12, 13) *Psarodictyum* sp. (12) Complete open conical to palmate specimen, with a pedunculated termination MMNHC 13265, scale bar 10 mm; (13) fragmented lamellate form showing thin walls, MMNHC 13266, scale bar 10 mm.

described by Raymond and Okulitch, 1940 from Sevier Formation (Upper Ordovician), east of Knoxville, Tennessee. The species was also reported from the San Juan Formation (Dapingian - Darriwilian) Cerro La Silla, Niquivil, and Villicum sections, San Juan Province, Argentine Precordillera (Carrera, 2003).

**Description.**—Long, cylindrical sponge, slightly expanded towards the top, with deep and wide spongocoel. Minimum diameter at the base 12 mm and a maximum diameter near the top 15 mm, with thin walls averaging 4 mm thick. Smooth, poorly preserved differentiated dermal layer composed of irregularly disposed monoclones mainly among external pores.

Fine anthaspidellid skeleton with a ladder-like appearance of the spicular mesh with the surface of skeletal trab divergence near the gastral surface. Very fine vertical trabs, united by small monoclone desmas (trab separation 0.2–0.3 mm), meet the external surface at high angles.

Horizontal radial canals, disposed in regular stalked series, range 0.3–0.5 mm in diameter. Some of the canals are slightly expanded at mid wall or near the gastral surface.

**Materials.**—Two almost complete specimens MMNHC 13263, MMNHC 13264.

**Remarks.**—The genus *Rhopalocoelia* Raymond and Okulitch, 1940 was erected to include tubular and cylindrical forms with an axial cavity that extends almost to the base, numerous branched radial canals, and a smooth exterior surface. Raymond and Okulitch (1940) proposed two species in the genus *Rhopalocoelia*. The type species, *Rhopalocoelia clarkii* Raymond and Okulitch, 1940, from New York and Vermont and *Rhopalocoelia regularis* Raymond and Okulitch, 1940 from Sevier Formation, east of Knoxville, Tennessee.

*Rhopalocoelia regularis* has a smaller spicule mesh than *R. clarkii*, and a more regular arrangement of canals, although they are sinuous and sometimes bifurcate, unlike how they are characterized in the genus diagnosis. Raymond and Okulitch (1940) described *R. regularis* as having large canals, which were sketched as being somewhat bulbous toward the gastral margin. De Freitas (1989), in his revision of some of the anthaspidellid genera, recognized large straight, not bulbous radial canals with a 0.4–0.6 mm diameter in *R. regularis*. We have observed in our material the same body form and canal morphology described by Raymond and Okulitch (1940) in their description of the type material of *R. regularis*, with canals straight and slightly expanded towards the gastral margin. *Rhopalocoelia regularis* reported from the Argentine Precordillera (Carrera, 2003) shows comparable external form and structural characteristics like those found in the type species. A well-preserved dermalia occurs in some Argentinean specimens, which is not as well developed in the Tennessee material.

Genus *Psarodictyum* Raymond and Okulitch, 1940

**Type species.**—*Psarodictyum magnificum* Raymond and Okulitch, 1940.

*Psarodictyum* sp.  
Figure 2.12, 2.13

**Occurrence.**—Lenoir Limestone (Upper Ordovician) East of Lenoir City, Loudon, Co., Tennessee.

**Description.**—Discoidal, open obconical to funnel-shaped sponge, ~20 cm in maximum diameter expanding upward from short stem-like area. Gastral and dermal surfaces generally smooth except for regular weak radial grooves and pits of aligned canal openings. Sponge wall thin (5 mm), with prominent radial canals (1 mm in average), and straight trabs in characteristic anthaspidellid structure. Plane of trab divergence at mid wall. Dendroclones disposed in slender ladder-like series; most spicules I-shaped, forming canal walls.

**Materials.**—One complete specimen MMNHC 13266 and a fragmentary specimen MMNHC 13265 from the Lenoir Limestone east of Lenoir City, Loudon Co., Tennessee, Upper Ordovician (Sandbian).

**Remarks.**—The poor preservation of the collected material prevents a more precise identification and description. However, the main characteristics observed are consistent with the assignment to the genus *Psarodictyum* Raymond and Okulitch, 1940.

*Psarodictyum magnificum* Raymond and Okulitch, 1940 from Valcour Island, New York and Mingan Island, Canada (Rigby and Desrochers, 1995) has a large, discoidal form, which is slightly different from the more conical to palmate grow form of the Tennessee specimens. *Psarodictyum planum* Raymond and Okulitch, 1940 is smaller, palmate, with a preserved stem area, but it has significantly coarser canals.

Sponges in the family Anthaspidellidae, Miller, 1889 (*Psarodictyum* Raymond and Okulitch, 1940 and *Patellispongia* Bassler, 1927) are both broad, saucer-shaped to open conical-shaped with thin walls. Both have a distinct radiate skeletal structure on both gastral and dermal surfaces. They lack the multiple openings that characterized the gastral surface of *Anthaspidella* Ulrich and Everett in Miller, 1889. However, clear distinction of these two genera is lacking, and *Psarodictyum* and *Patellispongia* could be synonyms. A comprehensive study of all species assigned to both genera is needed to clarify this possible synonymy, which is beyond the scope of this study.

Family Streptosolenidae Johns, 1994

**Remarks.**—The family Streptosolenidae was erected by Johns (1994) to circumscribe genera such as *Streptosolen*, *Lissocoelia*, and *Hesperocoelia* that bear a much more irregular and typically finer skeleton than those of the typical Anthaspidellidae (e.g., *Anthaspidella*, *Archaeoscyphia* or *Calicocoelia*). Although the radial canals may still appear vertically stacked, they are often sinuous and intertwining and frequently exit into vertical, axial apochetes. In addition, the endosomal spiculation contains a larger proportion of polyclone dendroclones or even rhizoclones, that frequently attach to each other instead of the trabs.

Johns (1994) also established that the dendroclones are often not horizontal where two trabs connect. Furthermore, the trabs that they connect may not be at the same depth within

the sponge wall. The result is a more complex, three-dimensional skeleton than other similar genera.

Genera included in the Streptosolenidae are separated from the Anthaspidellidae by the greater irregularity of their skeleton and the greater complexity of the canal systems that result. Apart from *Streptosolen*, *Lissocoelia*, and *Hesperocoelia*, other typical genera included in the Streptosolenidae are: *Allosacus*, *Aulocopium*, *Hudsonospongia*, and *Eospongia*.

Genus *Allosacus* Raymond and Okulitch, 1940

*Type species*.—*Allosacus proxilus* Raymond and Okulitch, 1940 from the Ottosee Limestone at Dickinson's Mill North of the Mendota Valley in Virginia, Tennessee and the Lenoir Limestone, Knoxville, Tennessee.

*Allosacus pedunculatus* new species  
Figure 3

*Type specimens*.—The complete holotype, MMNHC 13267 and a paratype MMNHC 13268 are both from the Lenoir Limestone east of Lenoir City, Loudon Co., Tennessee. Upper Ordovician (Sandbian).

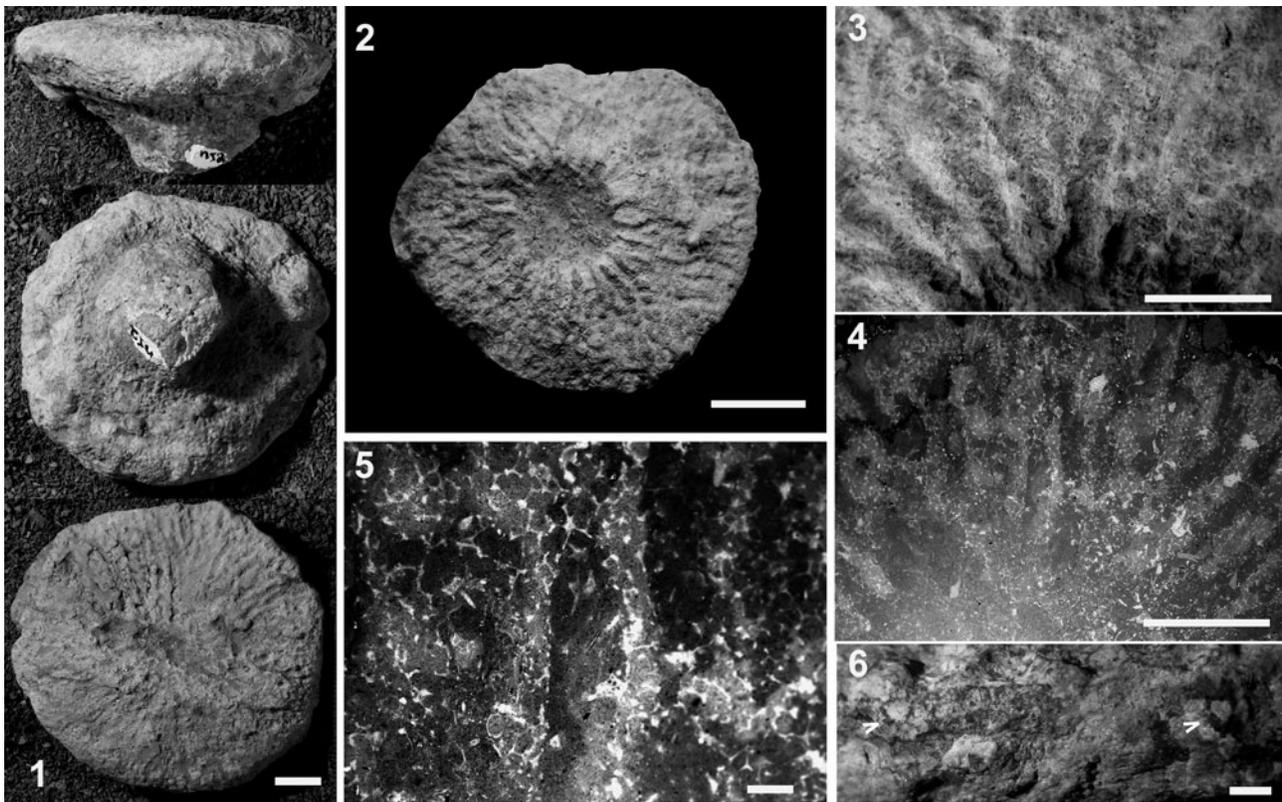
*Diagnosis*.—Discoidal pedunculate sponge, with convex upper surface, marked by large, sinuous and commonly branched radial canals that converge toward a central oscular depression.

Radial subsurface canals end as circular openings in the sponge margin. Skeleton composed by densely packed, dendroclone (monoclonid and polyclonid) spicules and loose spicules irregularly distributed in the walls between canals, “C-shaped” megascleres, and irregular tricloneid forms.

*Occurrence*.—Lenoir Limestone (Upper Ordovician) east of Lenoir City, Loudon, Co., Tennessee.

*Description*.—Discoidal to irregularly hemispherical and slightly pedunculated sponge, with convex upper surface. The greatest diameter is just above the base of the sponge. The maximum sponge diameter is 5 cm, 1.2 cm high, with an oscular diameter of 1.8 cm. The upper surface is marked by large, sinuous and commonly branched radial canals that converge toward a central oscular depression. These radial horizontal canals also occur below the main surface as small inhalant canals (0.8–1 mm in diameter). Radial subsurface canals end as circular openings in the sponge margin. The spicular mesh is mainly composed by densely packed, loose or welded dendroclone spicules. Among the loose spicules irregularly distributed in the walls between canals, “C-shaped” spicules and irregular “Y-shaped” forms rarely occur (Figs. 3, 5).

*Etymology*.—*Pedunculatus* from Latin, having a peduncle or stalk.



**Figure 3.** (1–6) *Allosacus pedunculatus* n. sp. (1) Lateral, ventral, and dorsal views of the holotype MMNHC 13267, a complete discoidal, pedunculated sponge, scale bar 10 mm; (2) dorsal view of the paratype MMNHC 13268 showing the shallow depression on top and the external radial grooves on the surface, scale bar 10 mm; (3) details of the previous photograph showing a closer view of the radial deep grooves, scale bar 5 mm; (4) transversal thin section showing the irregular, mostly radial spicular net, scale bar 5 mm; (5) enlargement of (4) showing the irregular distribution of varied dendroclone morphologies in the parietal walls, cut by radial canals, scale bar 1 mm; (6) lateral view of the external fringe of the sponge, showing emergence of radial canals as open rounded pits (arrows), scale bar 1mm.

*Remarks.*—*Allosacus proxilus* Raymond and Okulitch, 1940 was erected to include discoidal to mound-shape sponges with a central shallow oscular depression on top and radial canals marked as grooves in the upper surface converging towards the osculum. These characteristics are consistent with the material described in this contribution. However, in the type species, as well as in the *Allosacus* sp. described from Argentina (Carrera, 1996), the basal surface is flat to concave and completely used for attachment. This feature differs from the pedunculated morphology found in the material from the Lenoir Limestone. Furthermore, the discoidal margin in the type species and the specimen from Argentina (Carrera, 1996) bends downward forming the discoidal and completely attached base. This margin, in *A. pedunculatus* n. sp., is straight and relatively thick with marked openings for the radial canals emerging in the margin surface.

Genus *Zittelella* Ulrich and Everett, 1890

*Type species.*—*Zittelella typicalis* Ulrich and Everett, 1890.

*Remarks.*—*Zittelella* was not included by Johns (1994) in the family Anthaspidellidae nor in the family Streptosolenidae, although in the latter family he included the related genus *Hudsonospongia*. Finks and Rigby (2004) retained *Hudsonospongia* in the Streptosolenidae, but included *Zittelella* within the Anthaspidellidae.

*Zittelella* shows similar canal structure irregularity as that seen in *Hudsonospongia*, but bears a more complex spiculation, at least as it was described in detail for *Zittelella varians* (Billings, 1861) by Rigby and Desrochers (1995) from Mingan Island, Canada. The material described here, from Tennessee, is similar in this respect. Furthermore, like *Hudsonospongia*, *Zittelella* shows a scalariform, ladder-like spicule structure, but it is more irregular and scarcely marked, and the main choanosomal structure and canal walls are formed from irregularly distributed dendroclones (mainly Y and X shape). Unfortunately, the description and illustration of the spicular structure of the type species *Zittelella typicalis* Ulrich and Everett, 1890 are not informative enough for a definitive comparison. However, *Z. typicalis* shows more irregular dichotomous canals and the spiculation in vertical section as illustrated by Ulrich and Everett, (1890, fig 3a) shows clearly more irregularity than the regular ladder-like structure of anthaspidellids.

*Zittelella varians* (Billings, 1861)

Figure 4

*Type specimens.*—Holotype GSC 999f, h Clear Water Point, (La Grande Point) east side of Havre-Sainte Pierre, Canada (Billings, 1861).

*Occurrence.*—Lenoir Limestone (Upper Ordovician) East of Lenoir City, Loudon, Co., Tennessee and Mingan Island Quebec, Canada (Raymond and Okulitch, 1940; Rigby and Desrochers, 1995).

*Description.*—Small to intermediate-size sponges ranging from conical, to expanded obconical top-shaped. Small specimens

commonly pedunculated, 3 cm high and 2.9 cm in maximum diameter near the top of the sponge body. The largest specimen is open obconical, 4.3 cm high and 5.2 cm in maximum diameter near the top.

Upper surface with a shallow central depression including a moderately shallow spongocoel or oscular depression into which a cluster of vertical exhalant canals extends. External surface generally smooth, marked by shallow grooves of the radial canals on the flat top and by conspicuous pores over the rest of the sponge.

In longitudinal section, convergent horizontal canals arranged in vertically stacked regular rows, meet the spongocoel normally. The arching upward inhalant canals are ~1 mm in diameter and are vertically separated by a 2 mm thick parietal wall. Numerous vertical exhalant canals, 2 mm in diameter, extend from near the base of sponge to the base of oscular depression or spongocoel. These canals are separated by thin, one spicule thick walls, composed of monoclonid desmas and possibly monaxons.

The spongocoel is moderately deep, and occupies almost half of the sponge body (21 mm deep, measured from a specimen of 43 mm high). The maximum diameter is 25 mm located at the top of the sponge. Maximum wall thickness 15 mm, also near the top.

In transverse section, the oscular depression occupies half of the sponge diameter and is irregularly surrounded by circular openings of the axial vertical canals, 1.7–2 mm in diameter. The axial canals are separated by irregular walls that are 1–2 mm thick, but occasionally only a spicule thick.

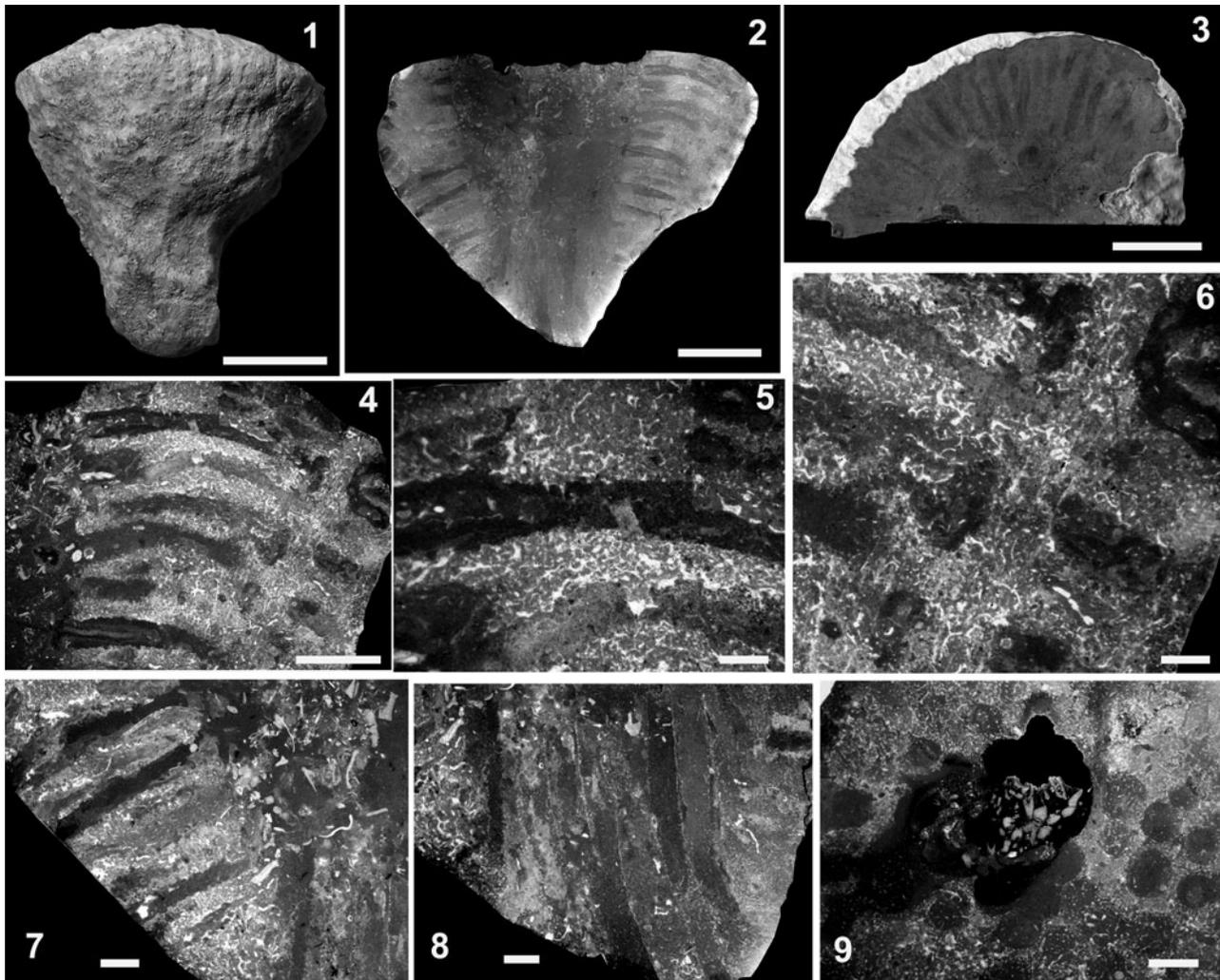
In general, the spicular skeleton is irregular and complex, dominated by I-shaped dendroclones in slightly marked ladder-like series. This basic skeleton is superposed by a complex irregular skeleton that forms thick horizontal canal walls. The skeleton around the canals is composed of irregularly disposed desmas (I-, Y-, X-, and H-shaped dendroclones; Fig. 4.5, 4.6), and most of these spicules bear curved and irregular terminations. C-shaped dendroclones also occur sporadically (Fig. 4.5, 4.6). Spicule length variable, 0.2–1.2 mm.

*Materials.*—Five complete specimens MMNHC 13269–13273.

*Remarks.*—The main distinctive features of *Zittelella varians* (Billings 1861) include: the overall stalked obconical to conico-cylindrical form, centrally located and moderately deep spongocoel or oscular depression into which a cluster of vertical exhalant canals extends subprismatically into circular openings, and convergent horizontal canals that are vertically stacked regular rows. Size of the spiculation and canal diameter are similar to those described for specimens from Mingan Island (Raymond and Okulitch, 1940; Rigby and Desrochers, 1995).

The type species *Zittelella typicalis* Ulrich and Everett, 1890 is very similar in size, form, and the distribution of canals. The primary difference relates to the shape of the spongocoel, which is very shallow in *Z. typicalis*, forming a simple central depression, into which the vertical canals open almost directly near the top of the sponge.

Other related species of the genus, such as, *Z. pannosa* Raymond and Okulitch, 1940 and *Z. grossa* Rigby and Desrochers,



**Figure 4.** (1–9) *Zittelella varians* (Billings, 1861). (1) Lateral view of a complete specimen, MMNHC 13269, scale bar 10 mm; (2) longitudinal thin section of a complete specimen, MMNHC 13270, showing vertically stacked radial canals, scale bar 10 mm; (3) transversal thin section showing straight radial canals, scale bar 10 mm; (4) detail of (2) showing the large radial canals and the irregular skeletal net, scale bar 5 mm; (5) detail of (2) showing parietal walls with irregularly distributed dendroclones, scale bar 1 mm; (6) enlargement of (4) showing a closer view of the parietal walls, including a visible vertical parietal with a faintly marked ladder-like distribution of dendroclones, scale bar 1 mm; (7) lower part of the sponge in (2) showing the radial canals at the base and the vertical canals from the base of the sponge, scale bar 2 mm; (8) vertical canals shown in the previous photograph, separated by very thin walls with a tiny alignment of “I-shaped” monocrepid dendroclones and possibly monaxons, scale bar 2 mm; (9) transversal view, specimen MMNHC 13271, showing the base of the central cavity and the appearance of the vertical canals, scale bar 2 mm.

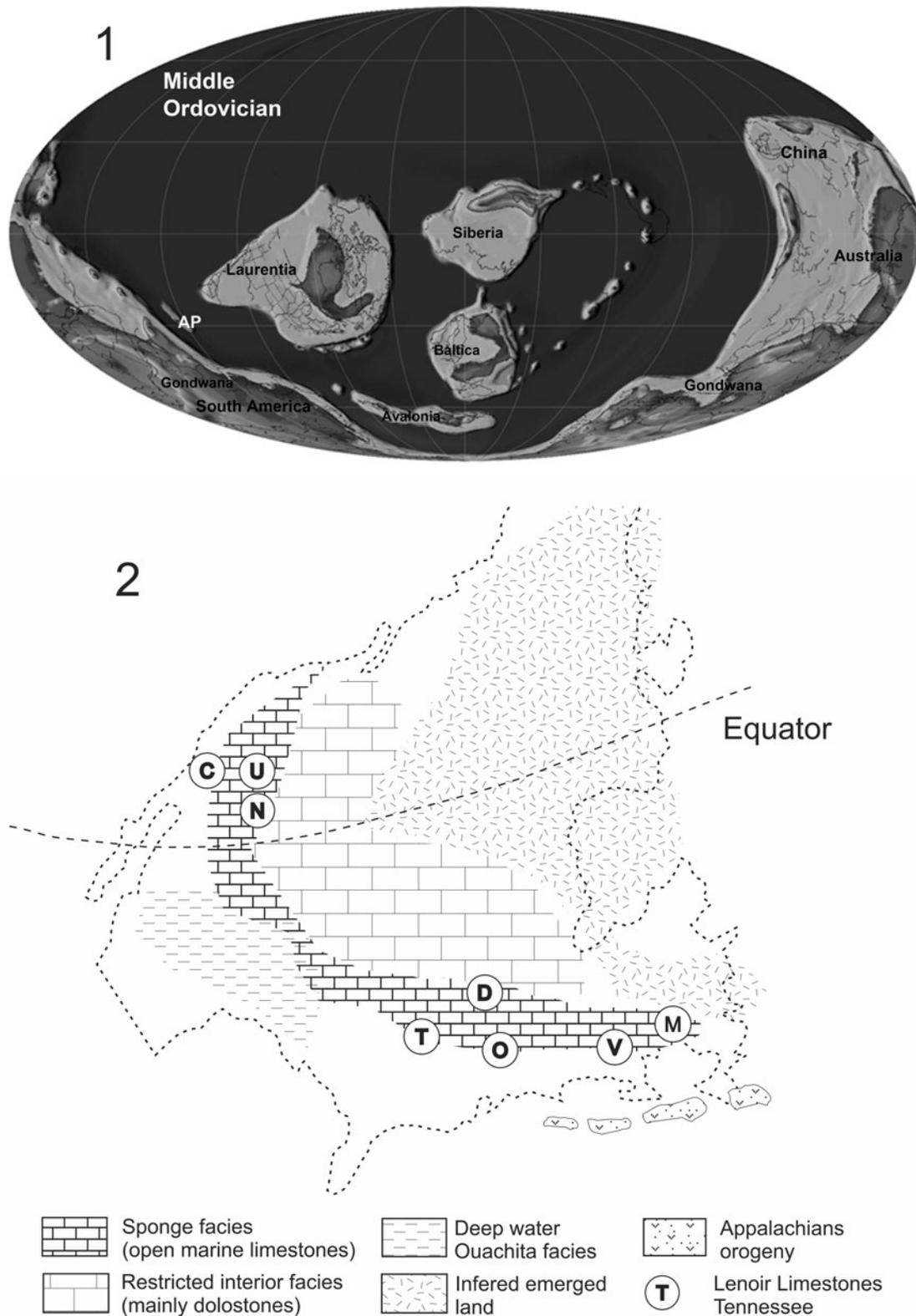
1995, show coarser spiculation and canals approximately twice the size of those seen in the Tennessee material.

### Paleobiogeographic significance of the Lenoir sponges

The first attempt to analyze the global distribution of Ordovician sponges, particularly those along the Laurentian margins, was performed by Carrera and Rigby (1999). Additional studies focusing on Ordovician sponge diversification patterns also incorporated paleobiogeographic information (Carrera and Rigby, 2004; Carrera and Botting, 2008; Muir et al., 2013). Updated information published subsequently confirms the overall paleobiogeographic pattern for sponge distribution in the Laurentian paleocontinent. Most of the more recent Ordovician sponge taxonomic studies are concentrated in areas outside of North America such as China, Korea, Morocco, and Wales with new data on protomonaxonid and orchoclad demosponges

and hexactinellids (Muir et al., 2013; Botting and Muir, 2018 and references therein).

Lower Ordovician sponge faunas have received more attention primarily because of increased study of reef systems mainly in China and Korea (Rigby et al., 1995; Wang et al., 2012; Choh et al., 2013; Adachi et al., 2015), confirming a global Lower Ordovician interval of reef recovery following the demise of archeocyaths. Lower Ordovician sponge faunas in North America, associated with reef structures, have been recorded in classical studies by Church (1974), Rigby and Toomey (1978), Toomey and Nitecki (1979), Pratt and James (1982), and Pratt (1989). Lower Ordovician bioherms usually built by microbes, sponges, and calathids occur in a broad belt along the southern and western margins of the North American continent, constituting the Laurentian sponge-algal facies (Alberstadt and Repetsky, 1989). Sponges associated with reef structures are recorded world-wide and are restricted to tropical or subtropical



**Figure 5.** (1) Middle Ordovician paleogeographic map showing position of Laurentia and nearby paleocontinents and terrains, AP: Argentine Precordillera (from Scotese, 2016). (2) Darriwilian to Sandbian paleogeographic map of Laurentia, showing main sponge localities and distribution of main lithofacies belts (after Alberstadt and Repetski, 1989) and inferred position of the equator. (M) Mingan Island, Quebec, Canada; (V) Valcour Island, New York; (D) Trenton limestone, Dixon, Illinois; (O) Ottosee Limestone, Virginia; (T) Lenoir limestones, Tennessee; (U) Utah; (N) Nevada; (C) California.

areas; with main occurrences in China and Korea (Rigby et al., 1995; Wang et al., 2012; Choh et al., 2013; Adachi et al., 2015; Li et al., 2015 and references therein), Siberia (Webby, 1984), Baltica (Kröger et al., 2017), and the Precordillera basin of Western Argentina (Cañas and Carrera, 1993; Carrera et al., 2017).

Most of the diverse Middle to Upper Ordovician sponge faunas are dominated by demosponges belonging to the families Anthaspidellidae and Streptosolenidae. Middle and Upper Ordovician (Darriwilian to Sandbian) faunas from eastern North America have been described from Tennessee, Virginia, Illinois, Quebec, Newfoundland, and in the Canadian Arctic (Raymond and Okulitch, 1940; Rigby, 1967a, 1977, 1995; Klappa and James, 1980; Rigby and Desrochers, 1995).

Middle Ordovician (Darriwilian) sponges have been reported from western North America in Utah, Nevada, and California (Bassler, 1941; Greife and Langenheim, 1963; Rigby, 1967b; Rigby and Chidsey, 1976; Johns, 1994).

Carrera and Rigby (1999) suggested an east-west differential distribution of Middle–Upper (Darriwilian to Sandbian) Ordovician demosponges along the Laurentian margins. These authors presented a compiled data set with fifteen demosponge genera described from Middle Ordovician rocks of eastern North America. Ten of these genera were not recorded in western North America and five were considered endemics. Eastern Laurentian faunas are dominated by several species of the anthaspidellid genera *Hudsonospongia*, *Psarodictyum*, *Rhopalocoelia*, and *Climacospongia*; the streptosolenids *Zittelella*, *Eospongia*, and *Allosacus*, and the megamorinid *Saccospongia* (see Tables 1, 2 for an updated sponge distribution).

**Table 1.** Middle and Upper Ordovician (Floian to Sandbian) generic sponge records in North America.

Middle and Upper Ordovician (Floian to Sandbian)	Western North America	Eastern North America
<b>Demosponges</b>		
<i>Allosacus</i>	—	x
<i>Archaeoscyphia</i>	x	x
<i>Anthaspidella</i>	x	x
<i>Calicocoelia</i>	x	x
<i>Eospongia</i>	—	x
<i>Hudsonospongia</i>	—	x
<i>Lissocoelia</i>	x	x
<i>Patellispongia</i>	x	x
<i>Psarodictyum</i>	—	x
<i>Rhopalocoelia</i>	—	x
<i>Streptosolen</i>	x	—
<i>Nevadocoelia</i>	x	—
<i>Hesperocoelia</i>	x	—
<i>Loganiella</i>	x	—
<i>Exocopora</i>	—	x
<i>Climacospongia</i>	—	x
<i>Zittelella</i>	—	x
<i>Saccospongia</i>	—	x
<i>Epiplastospongia</i>	—	x
<i>Colinispongia</i>	x	—
<i>Egania</i>	x	—
<i>Rugocoelia</i>	x	—
<i>Verpaspongia</i>	x	—
<b>Hexactinellid</b>		
<i>Asthenospongia</i>	x	—
<i>Cyathophycus</i>	x	—
<i>Pseudolancicula</i>	x	—
<b>Heteractinid (Calcarea)</b>		
<i>Toquimiella</i>	x	—

Carrera and Rigby (1999) recognized that the main components of the western Laurentian sponge association show an expansion of the streptosolenids, including several species of the endemic genera *Streptosolen*, *Hesperocoelia*, and *Verpaspongia*. Anthaspidellids are represented by some endemic forms, such as *Colinispongia* and *Egania*, as well as the occurrence of several species of the genera *Archaeoscyphia*, *Patellispongia*, and *Nevadocoelia*. This dataset along with an updated compiled dataset allowed Muir et al. (2013) to reach a similar conclusion. These authors also noticed that the Late Ordovician sponge faunas show an increasing differentiation along both margins, with the occurrence of hypercalcified sponges (Sphinctozoans), which are absent from the Atlantic side but are abundant on the Pacific side, with many genera shared with New

**Table 2.** Upper Ordovician (Katian–Hirnantian) generic sponge records in North America.

Upper Ordovician (Katian–Hirnantian)	Western North America	Eastern North America
<b>Demosponges</b>		
<i>Aulocopella</i>	—	x
<i>Archaeoscyphia</i>	—	x
<i>Aulocopium</i>	—	x
<i>Anthaspidella</i>	—	x
<i>Calicocoelia</i>	—	—
<i>Hindia</i>	x	x
<i>Hudsonospongia</i>	?	x
<i>Lissocoelia</i>	—	—
<i>Patellispongia</i>	—	x
<i>Psarodictyum</i>	—	—
<i>Streptosolen</i>	—	x
<i>Heterospongia</i>	—	x
<i>Steliella</i>	—	x
<i>Okulitchina</i>	—	x
<i>Ozarcocoelia</i>	—	x
<i>Cotylandia</i>	—	x
<i>Camellaspongia</i>	—	x
<i>Phiallaspongia</i>	—	x
<i>Edriospongia</i>	—	x
<i>Trichospongiella</i>	—	x
<i>Disctatospongia</i>	—	x
<i>Astylospongia</i>	—	?
<i>Caryospongia</i>	—	x
<b>Hexactinellids</b>		
<i>Brachiospongia</i>	—	x
<i>Cyathophycus</i>	x	x
<i>Tiddalickia</i>	—	x
<i>Acanthodictya</i>	—	x
<i>Teganium</i>	—	x
<i>Hydnodictya</i>	—	x
<i>Pyruspongia</i>	—	x
<i>Offella</i>	—	x
<i>Dierespongia</i>	—	x
<b>Heteractinids (calcarea)</b>		
<i>Astraeospongiium</i>	—	x
<i>Astraeoconus</i>	—	x
<i>Constellatospongia</i>	—	x
<b>Sphinctozoa (hipercalcified)</b>		
<i>Cliefdenella</i>	x	—
<i>Rigbyetia</i>	x	—
<i>Angulongia</i>	x	—
<i>Girtocoelia</i>	x	—
<i>Imperatoria</i>	x	—
<i>Corymbospongia</i>	x	—
<i>Cystothalamiella</i>	x	—
<i>Alaskaspongia</i>	x	—
<i>Porefieldia</i>	x	—
<i>Pseudoporefieldia</i>	x	—
<i>Amblysiphonella</i>	x	—
<i>Amblysiphonelloides</i>	x	—

South Wales (see Carrera and Rigby, 1999, 2004; Muir et al., 2013, and references therein).

The new records, described in this contribution, include genera previously recorded in the eastern North American margin, such as *Allosacus*, *Psarodictyum*, *Rhopalocoelia*, and *Zitelletta* reported from Mingan Island (Canada) and New York (Raymond and Okulitch, 1940; Rigby and Desrochers, 1995). *Rugocoelia* Johns, 1994, a typical genus from the western margin, is reported for the first time in Tennessee, although, a new species is erected maintaining a degree of differentiation at least at the species level.

These findings confirm the differential sponge faunal distribution along both Laurentian margins, because none of these forms has been reported from the western margin (present day orientation), even though some of these genera are recorded in nearby regions outside Laurentia, such as the Argentine Precordillera and Baltica (Carrera and Rigby, 1999). In addition, these genera were reported from a new different locality with almost the same sponge association as those found along Eastern North America, expanding the area, and suggesting a homogeneous distribution along the margin.

Carrera and Rigby (1999) explained this differential distribution as related to possible physical barriers that prevented the free distribution of sponges along the Laurentian continental margin. These include factors relating to the sedimentary nature of both margins as primary physical barriers and associated differential climatic constraints.

Physical barriers may relate to the development of the Mississippi embayment and southern Oklahoma aulacogens (see Marshak and Paulsen, 1996; Thomas, 2006 and references therein) that may have exerted a barrier effect in faunal distributions leading to the differentiation of the two sponge associations. The same restriction was inferred for the broad distribution of the Lower–Middle Ordovician sponge-algal facies along both Laurentian margins as reported by Alberstadt and Repetski (1989). The presence of the deep-water facies in these areas (Ouachita facies, see Alberstadt and Repetski, 1989) considerably narrowed the sponge-algal facies against the restricted facies developed in the epicontinental seas (Fig. 5).

The climatic constraint could relate to the more equatorial position of the Great Basin compared to the subtropical location of the Appalachian region (Witzke, 1990; Hodych et al., 2004; Pruss et al., 2010; Scotese, 2016, and references therein). Muir et al. (2013) emphasized the importance of this latitudinal position of Laurentia, and recognized that the western North American faunas have not been recorded elsewhere within the Middle Ordovician, and all of its characteristic faunal elements appear to have been endemic to the region. The paleocontinental reconstructions employed by Muir et al. (2013) locate western Laurentia within a tropical band, facing northwards towards the proto-Pacific Ocean, while the eastern Laurentia margin was positioned in a subtropical region facing southward towards the proto-Atlantic, Iapetus Ocean (Fig. 5).

By the Late Ordovician (Katian–Hirnantian), geographic sponge differentiation was more accentuated (Carrera and Rigby, 1999, 2004; Muir et al., 2013) with the occurrence of hypercalcified sponges in Western Laurentia (the Pacific association) in a clear subequatorial distribution and a remarkably different sponge association along the eastern margin (the Atlantic

association). In this Atlantic association, new suborders (Sphaerocladina, Tricranocladina, Rhizomorina, Megamorina) and families (Hindiidae, Chiastoclonellidae, Astylospongiidae, Haplistiidae) radiated and later became common elements of Silurian sponge faunas. The tectonic uplift of the Appalachians during the Upper Ordovician likely influenced the differentiation of the Atlantic sponge assemblages. The influence of the siliciclastic input is notable on this margin since the Middle Ordovician (see Miller and Mao, 1995). The worldwide peak in sponge diversity recorded during the late Ordovician is concentrated in areas of active tectonism and orogeny (Carrera and Rigby, 2004), and this signal is very strong in the Appalachian Basin.

There is a strong direct influence of environmental conditions and paleoecology on the sponge associations in more siliciclastic facies, such as those of the eastern margin of Laurentia. This may be one of the main differential constraints for sponge distribution, other than the latitudinal distinction.

Evidence based on sponge faunas is not conclusive during the Middle Ordovician—both margins share the same two main families of the orchoclad demosponges (Anthaspidellidae and Streptosolenidae) that are only differentiated at genus level. There are no clear paleoenvironmental conditions, at the scale of this analysis, that could satisfactorily explain this sponge differentiation. However, as it was pointed out above, and in the absence of other verifiable explanations, latitudinal climatic gradients are likely a factor in generation of the “north-south” Ordovician sponge distribution (Muir et al., 2013), which would also provide a way to keep the two sponge faunas distinct.

We are aware that other biological constraints of sponges (e.g., intrinsic ecological factors of the sponge species) could also be considered in this differential distribution (see for example Carrera and Rigby, 2004; Carrera and Botting, 2008; Muir et al., 2013). However, at the scale of the present analysis, intrinsic biological characteristics, other than larval distribution, appeared to be subordinate to large-scale, climatic or physical constraints.

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