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First record of conulariids from the Tērvete Formation, Upper Devonian of Latvia

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Abstract. Phosphatized remains belonging to conulariids have been found in the Middle Famennian (Upper Devonian) deposits of the Tērvete Formation of Latvia for the first time. The ornamentation pattern and characteristics of the exoskeleton indicate that the conulariids, represented by two incomplete and flattened specimens, belong to a single species within the genus *Paraconularia*. *Paraconularia* sp. from the Tērvete Formation differs from *Conularia latviensis* Delle from the Joniškis Formation in size and details of the morphology of the periderm; however, most probably, the species *C. latviensis* also belongs to the genus *Paraconularia*. Finding well-preserved almost complete conulariids agrees with the interpretation of sedimentation of the sandy deposits of the Tērvete Formation in the deltaic or estuarine settings.

Key words: Cnidaria, Scyphozoa, Conulariida, Devonian, Famennian.

INTRODUCTION

Conulariids are extinct marine animals with an almost global distribution and a fossil record from the Cambrian to the Late Triassic (Waterhouse 1979; Leme et al. 2008a, 2008b), and even possibly from the Ediacaran (Ivantsov & Fedonkin 2002; Van Iten et al. 2005, 2014, 2016). They were particularly diverse, reaching a maximum number of genera in the Ordovician. Conulariid fossils of intact specimens are not common, but sometimes may be found in large numbers of individuals, e.g. from the Upper Ordovician of the Prague Basin (Sendino et al. 2011) and the Middle Devonian of the New York State (Van Iten et al. 2013b). Instead, microscopic exoskeletal fragments are present in many beds, sometimes in very large numbers, e.g. in the Silurian Lower Visby Beds on Gotland (Jerre 1993).

Most part of conulariids secreted an elongate, four-sided steeply pyramidal, finely lamellar apatitic periderm (sometimes called theca) having a subtle bilateral symmetry. The length of the exoskeleton is usually 2–10 cm but may exceed even 50 cm (*Metaconularia papillata*; Ford et al. 2016). The wide end of the periderm is called the aperture, and the narrower end, if present, tapers into a near point apex with a tiny holdfast which is preserved only in bioimmured specimens (Vinn et al. 2019), or into an unornamented schott (apical wall). Well-preserved specimens of some conulariid species show lappets along the aperture centred on each of the four side faces. These lappets were flexible in a living animal, capable of folding inwards to close the periderm (Sendino et al. 2011; Ford et al. 2016). Thecae may be rectangular in the transverse cross section because the lateral sides differ in width, showing bilateral symmetry indicated also by different apical angles between the major (larger) and minor (smaller) faces of the periderm. It is also well seen in the differences in the pattern of transverse rib articulation between the major and minor faces. The weakly rectangular (almost square) outline of the conulariid exoskeleton in the cross section perpendicular to the long axis has given rise to the misconception that conulariids had a radial symmetry (Babcock 1993).

The exoskeleton was moderately flexible, being composed of numerous, thin apatitic laminae (Vinn & Kirsimäe 2015) alternating with thin organic-rich laminae (Ford et al. 2016). It was thickened in part by transverse thickenings that sometimes have been called rods, but in more recent works designated as transverse ribs and internal carina (e.g. Ford et al. 2016). In many conulariids, including most species of *Conularia* and *Paraconularia*, the faces show regular transverse ridges (ribs) that arch towards the aperture and bear a single row of regularly

spaced swellings, called nodes (e.g., Babcock & Feldmann 1986b; Van Iten 1992a; Ford et al. 2016). The trough-like area between the two adjacent transverse ribs is called the interspace. However, some conulariids (e.g., all species of *Metaconularia*) lack transverse ribs and exhibit rows of closely spaced nodes arching towards the aperture (Ford et al. 2016). The transverse ribs usually break in the midline. A longitudinal furrow along the corner where the two lateral faces meet, running the entire length of the periderm, is called the corner groove, or sulcus. In many species the midlines and/or corner sulci are sites of inwardly projecting carinae (e.g., Van Iten 1991, 1992a, 1992b; Ford et al. 2016). The midline carinae follow the same longitudinal path as the midline on the exterior surface of the theca.

The mode of life of conulariids has long been discussed. Exceptionally abundant specimens of *Conularia* aff. *desiderata* Hall, buried *in situ* in the marine argillaceous and silty very fine sandstone deposits of the Mount Marion Formation (Fm.) from the New York State, usually are solitary, but some occur in V-like pairs or in radial clusters consisting of three individuals (Van Iten et al. 2013b). Conulariids are oriented with their aperture facing obliquely upwards and with their long axis inclined at up to 87 degrees to bedding. This discovery supports the consensus that these animals were sessile, benthic organisms (e.g., Simões et al. 2003; Sendino et al. 2017).

Conulariid phylogenetic affinities have been argued for about 200 years. On the basis of specific morphology that does not seem to fit well into any one group, they have been described as molluscs, cnidarians, worms, vertebrates and as an independent phylum (for more references see Sendino et al. 2011). Few well-preserved specimens have been found with soft parts intact, e.g. tentacle-like structures extending from the aperture preserved in some Ediacaran specimens from China (Van Iten et al. 2013a). The modern consensus view is that the conulariids are an extinct group of cnidarians or have close affinities with cnidarians particularly more closely related to the polypoid coronate scyphozoans (Van Iten l992a; Van Iten et al. 2006; Leme et al. 2008a; Ford et al. 2016).

Late Ordovician and to a lesser extent Silurian conulariids occupied a stable place in the invertebrate assemblages of the Baltic palaeobasin. Their remains are particularly common in the Upper Ordovician deposits of Estonia, where conulariids were reported demonstrating symbiotic interactions with bryozoans (Vinn & Wilson 2015), and in the Silurian of Sweden (Jerre 1993). Conulariids have also been found in the Upper Devonian, Famennian deposits of Latvia (Gross 1933; Delle 1935, 1937; Liepiņš 1959): *Conularia* sp. in the Mūri and Žagare formations (Liepiņš 1959), as well as *Conularia latviensis* Delle, 1935 that has been described from the Joniškis Fm. However, conulariids were never recorded in the Tērvete Fm.

In the present paper two conulariid specimens found in the Famennian deposits of the Tērvete Fm., Latvia, are reported for the first time. The description of morphological features allows attributing both specimens to the conulariid genus *Paraconularia*. The Tērvete Fm., composed of the mainly siliciclastic deposits with thin layers of dolomitic marl, yields an assemblage of fossils represented by fish, charophyte algae and vascular plant remains, as well as rare trace fossils (Vasiļkova et al. 2012). The deposits of the formation were traditionally interpreted as having formed in a shallow, rather restricted sea of a lowered salinity (Savvaitova 1998) or even in conditions closer to the continental or the 'sea-lake' environment (Savvaitova 1977). However, the complex sedimentological and palaeontological study of the deposits of the Tērvete Fm. in the Klūnas outcrop allowed the conclusion that these sandy to clayey deposits were formed under the influence of fluvial and tidal processes in the shallow-water environment, at least partly as the infilling of erosional channels, thus evidencing deltaic or estuarine settings (Vasiļkova et al. 2012). The finding of conulariid fossils supports this interpretation of the sedimentary environment of the deposits of the Tērvete Fm.

GEOLOGICAL SETTING, MATERIAL AND METHODS

Both specimens were found in the Middle Famennian deposits of the Tērvete Fm. outcropping along the right bank of the Skujaine River downstream the Klūnas settlement in Zemgale, central Latvia (Fig. 1). The deposits of the Tērvete Fm. exposed here were accumulated in the northern part of the Baltic Devonian Basin, which during the Late Devonian was situated along the southern margin of the Euramerican continent close to the equator in the Southern Hemisphere. The Tērvete Fm. is composed of weakly cemented sandstone and sand intercalated with dolomitic marls, siltstone and clay, containing a relatively low-diversity assemblage of fish, charophytes and rare trace fossils determined by Delle (1937) as *Rhizocorallium devonicum*. The complete section of the formation reaches a maximum of 21 m in boreholes in the northeastern area of its distribution in Latvia. The section is at least 4 m thick in the Klūnas locality (Vasiļkova et al. 2012), which has been designated as the stratotype of the Tērvete Fm. (Savvaitova 1977). The Klūnas site is famous for its fauna of fishes, with abundant fossil remains in accumulations in sandy deposits (Lukševičs 2001; Vasiļkova et al. 2012).

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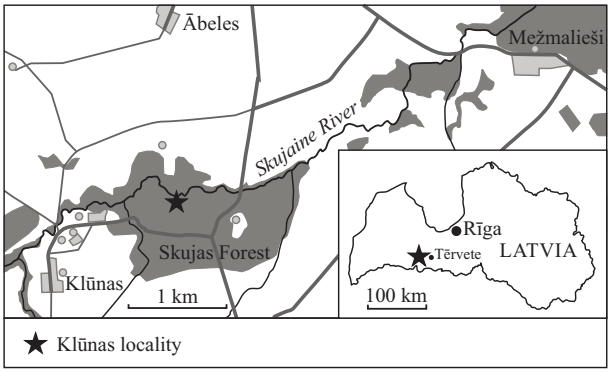

Fig. 1. Map of the vicinity of Tērvete showing the location of the Klūnas fossil site.

Stage	Conodont zones	Regional stages	Formations	Members	Placoderm zones
FAMENNIAN	*praesulcata*	Šķervelis	Šķervelis		
	expansa	Ketleri	Ketleri	Varkaļi	*Bothriolepis ciecere*
				Pavāri	
				Nīgrande	
	postera	Piemare	Žagare		interzone
			Sniķere		
	trachytera	Spārnene	● Tērvete		*Bothriolepis ornata*
	marginifera		Mūri		
		Akmene	Akmene		*Phyllolepis*
	rhomboidea	Kursa	Kursa		
	crepida	Joniškis	Joniškis		interzone
	triangularis	Šiauliai	Eleja	Sesava	
		Kruoja		Cimmermaņi	
				Purviņi	*B. leptocheira*

Fig. 2. Stratigraphic chart of the Famennian deposits of Latvia. Modified from Lukševičs et al. (2012) and Lukševičs & Stinkulis (2018). The black circle designates the stratigraphic level of this study.

restricted sea (sea-lake) of very low salinity (Savvaitova 1998). However, no direct indications of lowered salinity have ever been reported. The detailed sedimentological and taphonomical analysis of the geological section at the Klūnas site has shown that the deposits have formed under the influence of fluvial and tidal processes, in the deltaic or estuarine settings (Vasiļkova et al. 2012). The depositional environment is interpreted as the shallow-water environment, above the storm wave-base, where sand was accumulated in the subaqueous dunes which migrated downstream in a southerly direction. Erosional channels marked by the conglomerate containing clay clasts and vertebrate remains have been reported. The influence of the tidal processes on sedimentation was identified by mud and mica drapes on the cross-strata and by sandy and silty intercalations in the clayey deposits of the channel infillings.

A similar composition of sandy deposits, the restricted distribution of typical deposits of the Tērvete Fm. and a rather similar composition of vertebrate assemblages of the Mūri and Tērvete formations allowed L. Savvaitova to unite these formations, as well as the lower part of the Švėtė Fm. from Lithuania, into the corresponding Spārnene Regional Stage (Lukševičs et al. 1999; Fig. 2). Unfortunately, conodonts are not known from the Spārnene Regional Stage and its correlation with the Standard Conodont Zonation still remains unclear. Probably it coincides approximately with the *trachytera* and possibly *postera* conodont zones (Vasiļkova et al. 2012), judging from the position below the Sniķere Fm. which is the age equivalent of the Švėtė Fm. in Lithuania yielding a restricted assemblage correlated with the *postera* Zone (Middle–Lower *styriacus* zones of the previous conodont zonation; Žeiba & Valiukevičius 1972).

The material described here consists of two slabs of dolomitic marl with an admixture of silt and sand grains as well as of secondary calcite, of rhythmical lenticular structure, containing abundant ferruginated plant remains, rare trace fossils (*Rhizocorallium*?) and patchy accumulations of charophyte calcified oospheres, the gyrogonites, as well as two specimens of the conulariid periderm. The first one was found by chance in October 2017 during the collection of plant fossils in bed No. 8 (Vasiļkova et al. 2012, fig. 2). The other specimen was collected from the same bed in August 2018 during the excavations of fish and plant fossils. Slabs with abundant plant remains were collected by hammering, therefore, when splitting the rock, the skeleton of the first conulariid was broken and the outermost periderm surface remained mainly embedded on the reverse side of the other slab. The other specimen was not damaged during the collection; it shows the outer surface of the periderm, but it is less complete than the first specimen and much worse preserved. The main slabs were prepared mechanically under the stereomicroscope ZEISS KL 1500 LCD with a mounted needle. The reverse slab with the part of the first specimen was chemically prepared using the diluted acetic acid; unfortunately, as a result its outer surface became too fragile and mostly defoliated off the slab. The specimens were examined under the binocular optic microscope Leica Stemi 508 with digital camera Axiocam 208 housed in the Laboratory of Mineralogy and Palaeontology (MinPal), Faculty of Geography and Earth Sciences, University of Latvia. The specimens are housed at the Museum of University of Latvia, abbreviated LUGM 290. The terminology used in this paper is generally consistent with the terminology used by Van Iten (1992b) and Simões et al. (2003).

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Verrill, 1865
Class SCYPHOZOA Götte, 1887
Subclass CONULATA Moore & Harrington, 1956
Order CONULARIIDA Miller & Gurley, 1896
Family CONULARIIDAE Walcott, 1886
Genus *Paraconularia* Sinclair, 1940

Remarks. The genus *Paraconularia* is characterized by ridges that are generally widely spaced, usually 4 (3–5) rods per cm. More than 60% of the rods alternate at the midline; fewer than 40% abut. Apical angles are small, 9–28°. Nodes, adapertural spines and adapical spines may be present; if present, they are usually widely spaced, 2–6 units per mm (Babcock & Feldman 1986a).

Description. The studied conulariid sample LUGM 290-1015 is a 7.5 cm long and up to 4.3 cm wide, partially preserved periderm (Fig. 3). The periderm is horizontally oriented, completely flattened laterally (almost lenticular), which corresponds to the taphonomic model SCLa

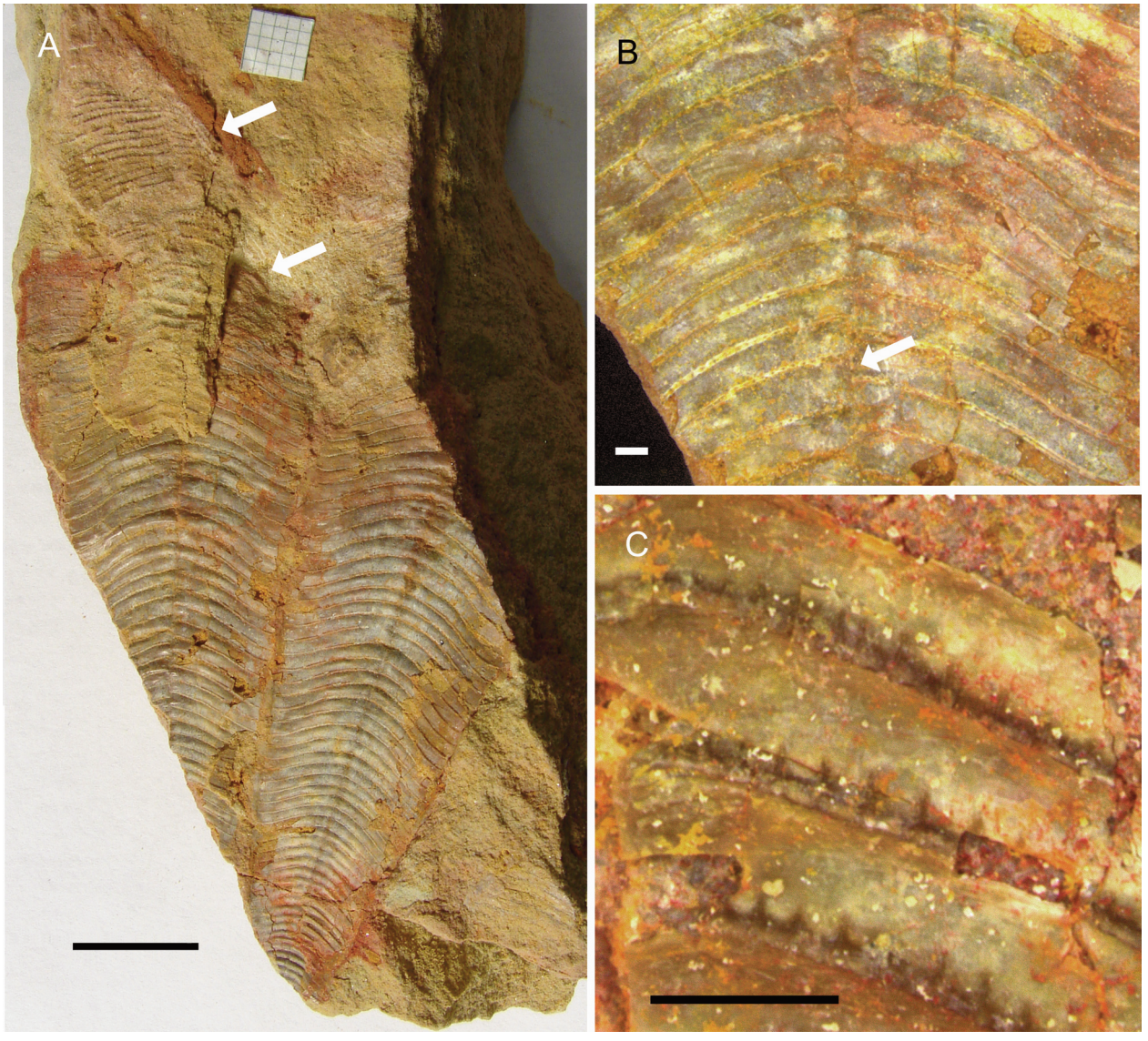

Fig. 3. Conulariid scyphozoan *Paraconularia* sp. LUGM 290-1015 from the Tērvete Formation, Middle Famennian, Upper Devonian, right bank of the Skujaine River downstream Klūnas settlement, Latvia. The specimen is oriented with the apertural end directed to the top of the page. **A**, the two exposed faces of the part of the specimen seen in visceral view, and possible lappet in outer view (upper white arrow). The lower white arrow is pointed to the major face. **B**, part of the major face with the white arrow pointed to the alternation of the transverse ridges. **C**, detail of the apertural region in the counterpart of the specimen in A, with relatively long spine-like nodes. Scale bars: 1 cm in A, 1 mm in B and C.

(according to Simões et al. 2003) and indicates the para-autochthonous or allochthonous mode of preservation. The peridermal space contains a small amount of fine sediments; there was a very thin (1–1.5 mm thick) layer of silt and sand particles between the walls, which could indicate the burial of the whole organism in the conditions of rapid sedimentation. The transverse ridges arch towards the aperture, forming a rounded convex curve (contrary to a Gothic arch or angular convex curve typical for the other genera). The interspaces are unusually wide; the number of ridges per 1 cm varies from 11–12 near the apex to 8–9 near the middle of the periderm and 12–13 (Fig. 3B) near the edge of the aperture. It is possible that the lappets are partially preserved at the distal end of the sample, because here the number of ribs increases sharply to 15–16 per 1 cm. Most of the transverse ridges (90%) in the middle of the major side wall do not touch, but alternate with each other in the glide reflection symmetry manner (Fig. 3B); in the minor side wall, the majority (85%) of the transverse ribs cross the middle continuously (Fig. 3A, right part). The transverse ridges are ornamented with relatively long, sloping-up (in living position), spine-like nodes (Fig. 3C). The nodes are arranged almost evenly on the side walls, but the distance between the nodes is variable and changes from 0.21 to 0.32 mm, or there are 4–6 nodes per 1 mm in the ridge. Incomplete preservation prevents accurate determination of the apical angle; the angle reaches approximately 21° for the major side wall and 17° for the minor side wall. Morphological features correspond to the definition of the genus *Paraconularia* (Babcock & Feldman 1986a); the fragmentary nature of the sample and lack of material for a biometric study make it impossible to identify the species.

DISCUSSION

Conulariids have previously been reported from several formations of the Upper Devonian, Famennian deposits of Latvia (Gross 1933; Delle 1937; Liepiņš 1959). The conulariid species *Conularia latviensis* Delle, 1937 was described on the basis of two specimens: (a) the holotype from the erratic boulder of dolostone belonging to the Upper Devonian Joniškis Fm., found in the Ruļļu Kalns esker (Liepiņš 1959 mentioned the same finding as belonging to the Kursa Fm., but most probably he was wrong) and (b) the specimen (Delle 1937; plate X, fig. 16) found in the dolomite quarry (nowadays abandoned) near Paugurkrogs and Berģi south of the city of Jelgava. In the same work Delle (1937) mentioned the finding of conulariids in the lowermost part of the so-called Venta complex, most probably corresponding to the Mūri Fm. of the modern stratigraphic chart. Later *Conularia* sp. from the Mūri Fm., cropping out at the right bank of the Svēte River near the Ķurbes farm and from the deposits of the Žagare Fm. in the borehole near the town of Liepāja, were reported (Liepiņš 1959).

The holotype of *Conularia latviensis* has not been found yet, but the second specimen figured by Delle (1937, plate X, fig. 16) is stored in the Museum of the University of Latvia (unnumbered specimen; M. Rudzītis, pers. comm. 2020). The characteristics mentioned in the description (Delle 1937) and personal observations made by the author of this article suggest that this species most probably belongs to the genus *Paraconularia*. However, *Paraconularia* sp. from the Tērvete Fm. differs from *Conularia latviensis* in a larger size, less frequently situated transverse ridges, their arrangement in the middle of the major side wall (ribs are continuous in *C. latviensis*), as well as the structure and location of the nodes. These differences do not allow the attribution of the studied *Paraconularia* sp. samples to the species *C. latviensis* Delle.

Conulariids generally occur in low-diversity assemblages (Babcock & Feldman 1986b), which evidences that they may have been be able to adapt to stressful living conditions and behave as opportunistic organisms (Bann et al. 2008); however, they are mainly reported from the deposits of marine origin. This agrees with the interpretation of the sedimentation of sandy clayey deposits of the Tērvete Fm. in the deltaic or estuarine settings (Vasiļkova et al. 2012), but totally contradicts the hypothesis about the sedimentation in the continental basin. The articulated nature of a very fragile conulariid material is also consistent with limited transportation after separation from the substrate, minimal post-depositional reworking and rapid burial. Usually taphonomically enhanced preservation occurs in sedimentary successions deposited under low rates of sedimentation interrupted by fast burial at or below storm wave base (Van Iten et al. 2014). However, most probably the Tērvete sandstones were deposited above the storm wave-base, and the changes in lithology from sandstone to dolomitic marls might indicate a short period of increase in the accommodation space due to a short transgression event.

CONCLUSIONS

For the first time, conulariid specimens have been found in the Middle Famennian Tērvete Fm. of Latvia. These specimens are attributed here to the genus *Paraconularia*. *Paraconularia* sp. from the Tērvete Fm. clearly differs from a slightly older *Conularia latviensis* from the Joniškis Fm. of Latvia; most probably, *Conularia latviensis* should be assigned to the genus *Paraconularia*. Finding well-preserved almost complete conulariids does not contradict

the interpretation of sedimentation of the sandy deposits of the Tērvete Fm. in the deltaic or estuarine settings.

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REFERENCES

Babcock, L. E. 1993. Exceptionally preserved conulariids from the Conularien-schichten, Fossil-Lagerstätten in the Devonian of Bolivia. In *Fosiles y Facies de Bolivia, Volume II – Invertebrados y Paleobotanica* (Suarez-Soruco, R., ed.), *Revista Tecnica de Yacimientos Petroliferos Fiscales Bolivianos*, **13**–**14**, 77–91.

Babcock, L. E. & Feldmann, R. M. 1986a. The phylum Conulariida. In *Problematic Fossil Taxa* (Hoffman, A. & Nitecki, M. H., eds), pp. 135–147. Oxford University Press, Oxford, New York.

Babcock, L. E. & Feldmann, R. M. 1986b. Devonian and Mississippian conulariids of North America. Part B. *Paraconularia*, *Reticulaconularia*, new genus, and organisms rejected from conulariida. *Annals of Carnegie Museum*, **55**, 411–479.

Bann, K. L., Tye, S. C., MacEachern, J. A., Fielding, C. R. & Jones, B. G. 2008. Ichnological and sedimentologic signatures of mixed wave- and storm-dominated deltaic deposits: examples from the Early Permian Sydney Basin, Australia. In *Recent Advances in Models of Siliciclastic Shallow-Marine Stratigraphy. SEPM Special Publication*, **90**, 293–332.

Delle, N. 1935. Zemgales līdzenuma, Augšzemes un Lietuvas devona nogulumi [Devonian deposits of the Zemgale Lowland, Augšzeme and Lithuania]. *Acta Universitatis Latviensis, Mathematics and Natural Sciences Series*, **2**(5), 105–384 [in Latvian and German].

Delle, N. 1937. Zemgales līdzenuma, Augšzemes un Lietuvas devona nogulumi [Devonian deposits of the Zemgale Lowland, Augšzeme and Lithuania]. *Acta Universitatis Latviensis, Mathematics and Natural Sciences Series*, **2**(5), separate issue: 106–384 [in Latvian and German].

Ford, R. C., Van Iten, H. & Clark II, G. R. 2016. Microstructure and composition of the periderm of conulariids. *Journal of Paleontology*, **90**, 389–399.

Götte, A. 1887. *Entwicklungsgeschichte der* Aurelia aurita *und* Cotylorhiza tuberculata. *Abhandlungen zur Entwicklungsgeschichte der Tiere*. Vol. 4, Verlag von Leopold Voss, Hamburg und Leipzig, 79 pp.

Gross, W. 1933. Die fische des Baltischen devons. *Palaeontographica*, **79A**, 1–74.

Ivantsov, A. Yu. & Fedonkin, M. A. 2002. Conulariid-like fossil from the Vendian of Russia: a metazoan clade across the Proterozoic/Palaeozoic boundary. *Palaeontology*, **45**, 1219–1229.

Jerre, F. 1993. Conulariid microfossils from the Silurian Lower Visby Beds of Gotland, Sweden. *Palaeontology*, **36**, 403–424.

Leme, J. M., Simões, M. G., Marques, A. C. & Van Iten, H. 2008a. Cladistic analysis of the suborder Conulariina Miller and Gurley 1896 (Cnidaria, Scyphozoa; Vendian/Triassic). *Palaeontology*, **51**, 649–662.

Leme, J. M., Simões, M. G., Rodrigues, S. C., Van Iten, H. & Marques, A. C. 2008b. Major developments in conulariid research: problems of interpretation and future perspectives. *Ameghiniana*, **45**, 407–420.

Liepiņš, P. 1959. *Famenskie otlozheniya Pribaltiki* [*Famennian Deposits of the Baltic States*]. Academy of Sciences of Latvian SSR, Riga, 139 pp. [in Russian].

Lukševičs, E. 2001. Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform. *Geodiversitas*, **23**, 489–609.

Lukševičs, E. & Stinkulis, Ģ. 2018. Pirmskvartāra nogulumieži un platformsegas uzbūve [Pre-Quaternary deposits and structure of the platform cover]. In *Latvija. Zeme, daba, tauta, valsts* [*Latvia. Land, Nature, People, Country*] (Nikodemus, O., Kļaviņš, M., Krišjāne, Z. & Zelčs, V., eds), pp. 38–58. Latvijas Universitātes Akadēmiskais apgāds, Riga [in Latvian].

Lukševičs, E., Mūrnieks, A. & Savvaitova, L. 1999. Subdivision of the Famennian Stage in the Baltic area by bio- litho- cyclostratigraphic methods. In *The Fourth Baltic Stratigraphical Conference, Problems and Methods of Modern Regional Stratigraphy, Abstracts* (Lukševičs, E., Stinkulis, Ģ. & Kalniņa, L., eds), pp. 56–58. University of Latvia, Rīga.

Lukševičs, E., Mūrnieks, A., Stinkulis, Ģ. & Popovs, K. 2012. Geological evolution of the Baltic Artesian Basin. In *Highlights of Groundwater Research in the Baltic Artesian Basin* (Dēliņa, A., Kalvāns, A., Saks, T., Bethers, U. & Vircavs, V., eds), pp. 7–52. University of Latvia, Riga.

Miller, S. A. & Gurley, W. G. E. 1896. New species of Paleozoic invertebrates from Illinois and other States. *Bulletin of the Illinois State Museum of Natural History*, 11, 1–50.

Moore, R. C. & Harrington, H. J. 1956. Conulata. In *Treatise on Invertebrate Paleontology, Part F, Coelenterata* (Moore, R. C., ed.), pp. F54–F66. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.

Savvaitova, L. 1977. *Famen Pribaltiki* [*Famennian of the Baltic States*]. Zinātne, Rīga, 128 pp. [in Russian].

Savvaitova, L. 1998. Tērvetes svīta [The Tērvete Formation]. In *The Encyclopaedia of Latvia's Nature, 5* (Kavacs, G., ed.), pp. 211–212. Preses Nams, Riga [in Latvian].

Sendino, C., Zágoršek, K. & Vyhlasová, Z. 2011. The aperture and its closure in an Ordovician conulariid. *Acta Paleontologica Polonica*, **56**, 659–663.

Sendino, C., Broda, K. & Zatoń, M. 2017. First record of true conulariids from the Upper Devonian of Poland. *Proceedings of the Geologists' Association*, **128**, 401–406.

Simões, M. G., Rodrigues, S. C., Leme, J. M. & Van Iten, H. 2003. Some Middle Paleozoic conulariids (Cnidaria) as possible examples of taphonomic artifacts. *Journal of Taphonomy*, **1**, 165–186.

Sinclair, G. W. 1940. The genotype of *Conularia*. *Canadian Field Naturalist*, **54**, 72–74.

Van Iten, H. T. 1991. Evolutionary affinities of the conulariids. In *The Early Evolution of Metazoa and the Significance of Problematic Taxa* (Simonetta, A. M. & Conway Morris, S., eds), pp. 145–155. Cambridge University Press, Cambridge.

Van lten, H. 1992a. Morphology and phylogenetic significance of the corners and midlines of the conulariid test. *Palaeontology*, **35**, 335–358.

Van Iten, H. 1992b. Microstructure and growth of the conulariid test: implications for conulariid affinities. *Palaeontology*, **35**, 359–372.

Van Iten, H., Leme, J. M., Rodrigues, S. C. & Simões, M. G. 2005. Reinterpretation of a conulariid-like fossil from the Vendian of Russia. *Palaeontology*, **48**, 619–622.

Van Iten, H., Leme, J. M., Simões, M. G., Marques, A. C. & Collins, A. G. 2006. Reassessment of the phylogenetic position of conulariids (Ediacarian–Triassic) within the subphylum Medusozoa (phylum Cnidaria). *Journal of Systematic Palaeontology, Inglaterra*, **4**, 109–118.

Van Iten, H., Leme, J. M., Marques, A. C. & Simões, M. G. 2013a. Alternative interpretations of some earliest Ediacaran fossils from China. *Acta Palaeontologica Polonica*, **58**, 111–113.

Van Iten, H., Tollerton Jr., V. P., Ver Straeten, C. A., Leme, J. M., Simões, M. G. & Rodrigues, S. C. 2013b. Life mode of *in situ Conularia* in a Middle Devonian epibole. *Palaeontology*, **56**, 29–48.

Van Iten, H., Marques, A. C., Leme, J. M., Pacheco, M. L. A. F. & Simões, M. G. 2014. Origin and early diversification of the phylum Cnidaria Verrill: Major developments in the analysis of the taxon's Proterozoic–Cambrian history. *Palaeontology*, **57**, 677–690.

Van Iten, H., Leme, J. M., Pacheco, M. L. A. F., Simões, M. G., Fairchild, T. R., Rodrigues, F., Galante, D., Boggiani, P. C. & Marques, A. 2016. Origin and early diversification of Phylum Cnidaria: key macrofossils from the Ediacaran System of North and South America. In *The Cnidaria. Past, Present and Future* (Goffredo, S. & Dubinsky, Z., eds), pp. 31–40. Springer International Publishing.

Vasiļkova, J., Lukševičs, E., Stinkulis, Ģ. & Zupiņš, I. 2012. Taphonomy of the vertebrate bone beds from the Klūnas fossil site, Upper Devonian Tērvete Formation of Latvia. *Estonian Journal of Earth Sciences*, **61**, 105–119.

Verrill, A. E. 1865. Classification of polyps (extract condensed from Synopsis of the Polyps and Corals of the North Pacific Exploring Expedition under Commodore C. Ringgold and Captain John Rogers, U. S. N.). *Communications of the Essex Institute*, **4**, 145–152.

Vinn, O. & Kirsimäe, K. 2015. Alleged cnidarian *Sphenothallus* in the Late Ordovician of Baltica, its mineral composition and microstructure. *Acta Palaeontologica Polonica*, **60**, 1001–1008.

Vinn, O. & Wilson, M. A. 2015. Symbiotic interactions in the Ordovician of Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **436**, 58–63.

Vinn, O., Ernst, A., Wilson, M. A. & Toom, U. 2019. Symbiosis of conulariids with trepostome bryozoans in the Upper Ordovician of Estonia (Baltica). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **518**, 89–96.

Walcott, C. D. 1886. Studies on the Cambrian faunas of North America. *Bulletin of the United States Geological Survey*, 30, 731–1095.

Waterhouse, J. B. 1979. Permian and Triassic conulariid species from New Zealand. *Journal of Royal Society of New Zealand*, **9**, 475–489.

Žeiba, S. & Valiukevičius, J. 1972. New data on the Famennian conodonts of the southern Baltic. *Trudy Vysshykh Shkol Litovskoj SSR, Geografiya Geologiya* [*Papers of High Schools of Lithuanian SSR, Geography, Geology*], **9**, 167–171 [in Russian].

Konulariidide esmaleid Ülem-Devoni Tērvete kihistust Lätis

Ervīns Lukševičs

On kirjeldatud fosfaatsete konulariidide esmaleidu Kesk-Famenne'i (Ülem-Devon) Tērvete kihistust Lätis. Kahe fragmentaarse ja deformeeritud eksemplari ornamentatsioon ning välisskeleti tunnused näitasid, et tegemist on liigiga perekonnast *Paraconularia*. Tērvete kihistust leitud materjal erineb varasemalt tuntud Joniškise kihistu liigist *Conularia latviensis* mõõtmete ja peridermi morfoloogia poolest. Siiski kuulub *C. latviensis* tõenäoliselt samuti perekonda *Paraconularia*. Artiklis kirjeldatud leid kinnitab varasemaid interpretatsioone, et Tērvete kihistu liivakad setted kuhjusid delta või estuaari keskkonnas.