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FIRST OCCURRENCE OF THE GENUS *SPHENOTHALLUS* HALL, 1847 (CNIDARIA) IN THE CARBONIFEROUS OF THE DNIPRO-DONETS DEPRESSION, UKRAINE

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ABSTRACT – The first occurrence of the problematic cnidarians *Sphenothallus* Hall (*S*. sp. 1 and *S*. sp. 2) is described from upper Viséan and ?Bashkirian (Carboniferous) black shales of the Dnipro-Donets Depression in NE Ukraine. Carboniferous *Sphenothallus* spp. from the Dnipro-Donets Depression apparently led an epifaunal gregarious lifestyle, preferring paleobasin areas with slow sedimentation rates, low current energy, and dysaerobic environments, as already suggested by literature data. The discovery of representatives of the genus *Sphenothallus* in Carboniferous strata of Ukraine significantly extends our knowledge about the geographic distribution of these animals. Further, it confirms their preference for environments with slow sedimentation.

Keywords: cnidarians, *Sphenothallus*, Carboniferous, Dnipro-Donets Depression, Ukraine.

RESUMO – Neste artigo é descrita a primeira ocorrência de cnidários problemáticos *Sphenothallus* Hall (*S*. sp. 1 e *S*. sp. 2) em folhelhos negros do Viseano Superior e ?Bashkiriano (Carbonífero), da Depressão de Dnipro-Donets, no NE da Ucrânia. *Sphenothallus* spp. carboníferos da Depressão de Dnipro-Donets foram, aparentemente, invertebrados gregários epifaunais, preferindo áreas da paleobacia com baixas taxas de sedimentação e baixa energia hídrica, em ambientes disaeróbio, conforme já sugeridos por dados de literatura. A descoberta de representantes do gênero *Sphenothallus* nos estratos carboníferos da Ucrânia amplia significativamente o nosso conhecimento sobre a distribuição geográfica desses animais e confirma, ainda mais, sua preferência por condições de baixa taxa de sedimentação.

Palavras-chave: cnidários, *Sphenothallus*, Carbonífero, Depressão de Dnipro-Donets, Ucrânia.

INTRODUCTION

Macroscopic, elongate, tubicolous phosphatic fossils assigned to the genus *Sphenothallus* Hall, 1847 are known in Paleozoic marine sediments in many parts of the world, including North America (Mason & Yochelson, 1985; Bodenbender *et al*., 1989; Frey, 1989; Van Iten *et al*., 1992; Neal & Hannibal, 2000 and references there), Greenland (Peel, 2021), South America (Clarke, 1913; Taboada, 1997; Van Iten *et al*., 2019), Africa (Van Iten *et al*., 2016), Europe (Nathorst, 1883; Fauchald *et al*., 1986; Brood, 1988; Fatka *et al*., 2012; Stewart *et al*., 2015; Vinn & Kirsimäe, 2015; Vinn & Mironenko, 2021; Halamski *et al*., 2022 and references in these works), and Asia (Choi, 1990; Zhao *et al*., 1999; Yi *et al*., 2003; Wang *et al*., 2003; Li *et al*., 2004; Van Iten *et al*., 2013; Muscente & Xiao, 2015; Dzik *et al*., 2017; Chang *et al*., 2018 and references therein).

Representatives of this genus are characterized by a gently tapered, finely lamellar phosphatic tube with a subconical holdfast and a pair of lateral thickenings (Zhu *et al*., 2000; Van Iten *et al*., 2002). These fossils are often found in marine black shales originated in dysoxic environments (*e.g*., Feldmann *et al*., 1986; Van Iten *et al*., 1992, 1996; Bolton, 1994; Neal & Hannibal, 2000; Van Iten *et al*., 2002; Peng *et al*., 2005; etc.), but sometimes occur in shallow carbonate rocks, even in archaeocyathan bioherms (Li *et al*., 2004). There is an occurrence of a single allochthonous tube of *Sphenothallus* sp. in lacustrine black shales (Lerner & Lucas, 2011). Tubes of *Sphenothallus* encrust various hard substrates, including brachiopod shells (Neal & Hannibal, 2000) and carbonate hardgrounds (Bodenbender *et al*., 1989). *Sphenothallus* ranges from the Cambrian to the Triassic (Van Iten *et al*., 2023).

In the Carboniferous, representatives of the genus *Sphenothallus* were distributed mainly in the northern hemisphere (Table 1) and are represented by three species, *S. bicarinatus* (Girty, 1911), *S. carbonarius* (M'Coy, 1844), and *S. stubblefieldi* Schmidt & Teichmüller, 1956.

Originally, *Sphenothallus* was classified as a plant (Hall, 1847), but later these fossils were attributed to conulariids, hydroids, annelids, or graptolites (Price, 1920; Mason & Yochelson, 1985; Feldmann *et al*., 1986; Choi, 1990; Lerner & Lucas, 2011; Van Iten *et al*., 2019, etc.). *Sphenothallus* is

Table 1. Carboniferous record of the genus *Sphenothallus* Hall, 1847.

Locality	Age	Taxa	References
Russia	Serpukhovian	*S.* cf. *angustifolius*	Vinn & Mironenko, 2021; Vinn, 2022
Ukraine	Late Viséan	*S.* sp.	This study
	?Bashkirian	*S.* sp.	
	Bashkirian	*S.* sp.	Dernov & Udovychenko, 2019
Poland	Bashkirian	*S. carbonarius*	Korejwo & Teller, 1972
		S. stubblefieldi	Korejwo & Teller, 1968
Czech Republic	Bashkirian	*S. carbonarius*	Řehoř & Řehořová, 1972
Germany	Serpukhovian	*S. stubblefieldi*	Schmidt & Teichmüller, 1958
	Pennsylvanian	*S. stubblefieldi*	Schmidt & Teichmüller, 1956
	Bashkirian	*S. bicarinatus*, *S. carbonarius*, *S. stubblefieldi*	Schmidt & Teichmüller, 1958
France	Bashkirian	*S.* sp.	Schmidt & Teichmüller, 1958
Belgium	Serpukhovian	*S. bicarinatus, S. carbonarius, S. stubblefieldi*, *S.* sp.	Schmidt & Teichmüller, 1958
	Bashkirian	*S. stubblefieldi*	Schmidt & Teichmüller, 1958
Netherlands	Bashkirian	*S. stubblefieldi*	Schmidt & Teichmüller, 1958
England	Bashkirian	*S. stubblefieldi*	Schmidt & Teichmüller, 1956
	Mississippian	*S. carbonarius*	Etheridge, 1880
	Serpukhovian	*S. carbonarius*	Wilson, 1967
Ireland	Mississippian	*S. carbonarius*	M'Coy, 1844
United States	Serpukhovian	*S.* sp.	Grogan & Lund, 2002
		S. bicarinatus, *S. carbonarius*	Mason & Yochelson, 1985
		S. bicarinatus	Elias, 1958
		S. sp.	Van Iten et al., 1992
		S. bicarinatus	Girty, 1911
	Moscovian	*S.* sp.	Girty, 1915
	Kasimovian	*S.* sp.	Lerner & Lucas, 2011
Argentina	(?)Moscovian–Gzhelian	*S. stubblefieldi*	Taboada, 1997

currently classified as a hydrozoan or scyphozoan cnidarian (Van Iten *et al*., 1992, 2002, 2013).

Previously, representatives of the genus *Sphenothallus* had not been described from the territory of Ukraine. Only a minor work by the present author and Mykola Udovychenko (Dernov & Udovychenko, 2019) cites fossils identified as cf. *Sabellidites* sp. from the Mospyne Formation (upper Bashkirian) of the Donets Basin, eastern Ukraine. These fossils apparently belong to the genus *Sphenothallus*. The macrofaunal remains mentioned by Dernov & Udovychenko (2019) were found in black shales formed in shallow-marine dysaerobic conditions (see Dernov & Udovychenko, 2019 for more details).

The Carboniferous macrofauna of the Dnipro-Donets Depression in NE Ukraine is poorly understood, as the multi-kilometer-thick Carboniferous succession occurs at considerable depths. The biostratigraphy of the Mississippian sedimentary succession in the Dnipro-Donets Depression, with which gas and oil deposits are associated, is based mainly on foraminifers and palynoflora (Brazhnikova *et al*., 1967; Poletaev *et al*., 1991). However, studying the Carboniferous macroscopic fossils of the Dnipro-Donets Depression is important for detailed paleoecological studies and improving the Carboniferous biostratigraphy.

Here I describe the first record of *Sphenothallus* from the Carboniferous strata of the Dnipro-Donets Depression in NE Ukraine. The new finds expand the geographical distribution of the genus *Sphenothallus* and broaden the known paleontological characteristics of the Carboniferous (Viséan–Bashkirian) sedimentary rocks of the Dnipro-Donets Depression.

MATERIAL AND METHODS

Three core samples (specimens IGS NASU-19/01 to IGS NASU-19/03) with remains of *Sphenothallus* spp. from Mississippian and Bashkirian strata of the Dnipro-Donets Depression were investigated in the present study. This material (collection IGS NASU-19) is stored in the Department of Paleontology and Stratigraphy of the Paleozoic Sediments, Institute of Geological Sciences (National Academy of Sciences of Ukraine, Kyiv).

The studied fossils come from three localities (Figure 1): (1) Ukraine, Chernihiv Region, Voloshky oil and gas field near Talalayivka, borehole Voloshky-2 (depth 4799.0–4811.0 m); upper Viséan black shale with clusters of *Sphenothallus* sp. 1 (specimen IGS NASU-19/01) and rare shells of productide brachiopods on bedding planes; (2) Ukraine, Poltava Region, Bil's'ke oil and gas field near Zin'kiv, borehole Bil's'ka-470 (depth 4456.0–4469.0 m); upper Viséan black shale with tubes of *Sphenothallus* sp. 2 (specimen IGS NASU-19/03); (3) Ukraine, Poltava Region, Novomykolayivs'ke oil and gas field near Novi Sanzhary, borehole no. 22-k (depth 1034.0–1044.0 m); siderite concretion from the ?Bashkirian black shale with *Sphenothallus* sp. 1 (specimen IGS NASU-19/02) and a shell of a rhynchonelloid brachiopod.

Unfortunately, it was not possible to determine from which particular upper Viséan and Bashkirian formation of the Dnipro-Donets Depression the studied material originates. It was given by (presently) unknown geologists in the 1970s and 1980s to the staff of the Department of Stratigraphy and Palaeontology of the Paleozoic Sediments (Institute of Geological Sciences of the NAS of Ukraine, Kyiv) for study, but until now, it remained unstudied.

Institutional abbreviations: IGS NASU, Institute of Geological Sciences, National Academy of Sciences of Ukraine, Kyiv.

GEOLOGICAL SETTING

The studied remains of *Sphenothallus* come from two facial zones of the Dnipro-Donets Depression (*sensu* Poletaev, 2013): the Chernihiv-Valky facial Zone (boreholes Voloshky-2 and Bil's'ka-470) and the Lelyakivka-Oril' facial Zone (borehole no. 22-k).

The Viséan strata (Artyukhivka, Solokhy, Moshkivka, Andriyashivka, Perekopivka, and Vasyl'kivka formations) in the Chernihiv-Valky facial Zone consist mainly of sandstones, mudstones, siltstones, limestones, dolomites, and coals with a predominance of marine sediments. Mudstones are dark gray, partly calcareous, and carbonaceous with miospores, plant debris, and marine fauna (*e.g*., brachiopods, bryozoans, crinoids, ostracods). The siltstones are dark gray, micaceous and clayey; the sandstones are gray and dark gray, fine-grained, quartz and micaceous, and sometimes dolomitized. The limestones are dark gray, pelitomorphic, detrital, and in some cases argillaceous with foraminifers, sponges, corals, brachiopods, bryozoans, crinoids, ostracods, and calcareous algae. Some limestones contain coral and bryozoan bioherms (Poletaev *et al*., 1991; Poletaev & Vdovenko, 2013).

The Bashkirian sedimentary succession (*i.e*., Velyki Bubny Formation and unnamed age-equivalent strata of the Mospyne, Smolyanynivka, and Belaya Kalitva formations of the Donets Basin, eastern Ukraine) in the Lelyakivka-Oril' facies Zone are represented by marine and continental sediments, namely limestones, sandstones, mudstones, siltstones, and coals. The limestones are gray, crystalline, and detrital with foraminifers, sponges, brachiopods, bryozoans, bivalves, crinoids, ostracods, conodonts, and calcareous algae. The mudstones are dark gray, micaceous, and contain plant debris. The sandstones are carbonate-quartz and feldspar-quartz; the siltstones are gray, micaceous, carbonaceous, and calcareous (Poletaev *et al*., 1991; Nemyrovska & Yefimenko, 2013).

SYSTEMATIC PALEONTOLOGY

Phylum CNIDARIA Hatschek, 1888
Subphylum MEDUSOZOA Peterson, 1979
Class, Order, and Family uncertain

Sphenothallus Hall, 1847

1839 *Serpuloides*: Sowerby in Murchison, p. 608.
1839 *Serpulites*: Sowerby in Murchison, p. 608.
1856 *Campylites*: Eichwald, p. 409.
1896 *Enchostoma*: Miller & Gurley, p. 29.
1949 *Tubulelloides*: Howell, p. 2.

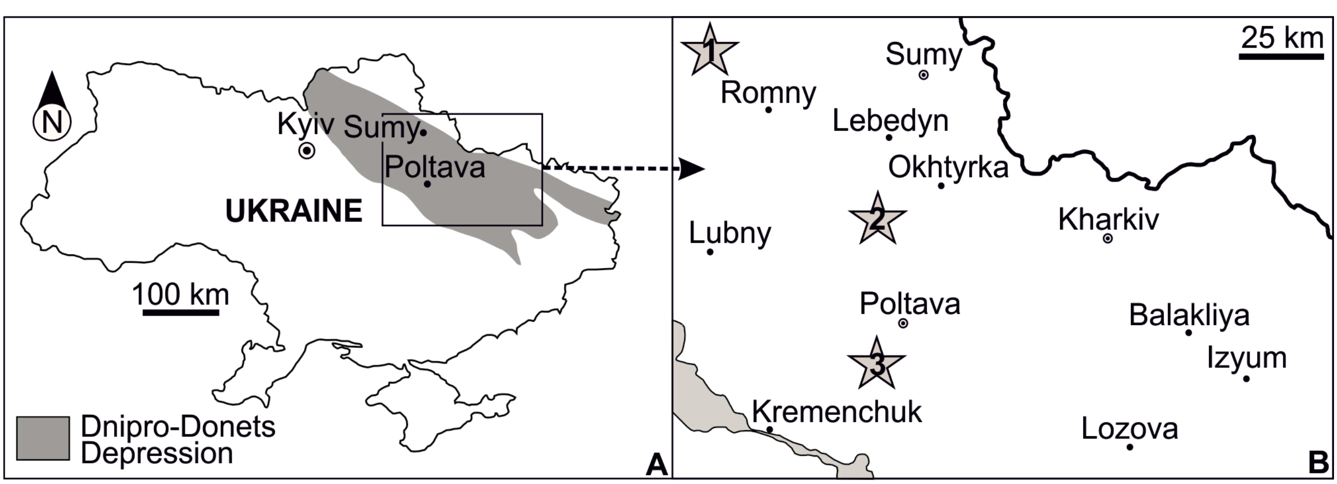

Figure 1. Geographic location of the *Sphenothallus*-bearing sites in the Dnipro-Donets Depression (marked by asterisks): **1**, borehole Voloshky-2; **2**, borehole Bil's'ka-470; **3**, borehole no. 22-k.

For a more detailed discussion on the synonymy of *Sphenothallus* see Mason & Yochelson (1985), Neal & Hannibal (2000), and Zhu *et al*. (2000).

Type species. *Sphenothallus angustifolius* Hall, 1847; original designation.

Diagnosis. "Theca slender, elongate (up to 90 mm or greater in length), single or branched, with a small, subconical holdfast and a pair of robust, longitudinal thickenings that extend from the holdfast to the aperture. Theca apatitic or (possibly) organic, finely, and continuously lamellar, with the lamellae arranged parallel to the thecal surface. Theca commonly curved in the apical region, elsewhere more or less straight, with a low rate of apertural expansion (range approximately 2–23°). Inner surface smooth; outer surface smooth or with numerous, closely spaced, transverse ridges or striae that are straight or gently curved toward the aperture; transverse ridges or striae may be restricted to the thin wall between the longitudinal thickenings, or they may cross both the thin wall and the thickenings. Apertural end open, with a smooth margin that may arch beyond the ends of the longitudinal thickenings. Transverse cross section subcircular in the immediate vicinity of the basal attachment disk, elsewhere elliptical. Basal attachment disk subconical and consisting of a thick, cone-like upper part and an extremely thin, flat base. Longitudinal thickenings centered on the end points of the theca's widest diameter and extending almost its entire length; outer surface of the longitudinal thickenings subangular or rounded in transverse cross section, inner surface concave. Interior of the theca may contain a thin, finely lamellar, transverse wall that is convex toward the apical end and extends along the inner surface of the theca proper, toward the aperture" (after Zhu *et al*., 2000: p. 229).

Included species. *Sphenothallus angustifolius* Hall, 1847 (Ordovician); *S. bicarinatus* (Girty, 1911) (Carboniferous); *S. carbonarius* (M'Coy, 1844) (Carboniferous); ?*S. kordulei* Fatka *et al*., 2012 (Cambrian); *S. kozaki* Fatka *et al*., 2012 (Cambrian); *S. kukersianus* (Öpik, 1927) (Ordovician); *S. longissimus* (Sowerby in Murchison, 1839) (Silurian); *S. pleijeli* (Brood, 1988) (Silurian); *S. ruedemanni* (Kobayashi, 1934) (Ordovician); *S. sica* (Salter, 1856) (Devonian); *S. songlinensis* Peng *et al*., 2005 (Cambrian); *S. stubblefieldi* Schmidt et Teichmüller, 1956 (Carboniferous); ?*S. taijiangensis* Zhu *et al*., 2000 (Cambrian). Many of these species are surely synonymous, so a revision is necessary.

Remarks. *Martsaphyton* Tinn *et al*., 2020 most closely resembles *Sphenothallus* in its phosphatic composition and lamellar skeleton structure, but it differs from *Sphenothallus* in having rootlike appendages and a wide apertural chamber and in lacking lateral thickenings of the tube wall (Tinn *et al*., 2020). A pair of marginal thickenings partially distinguishes *Sphenothallus* from all other tubular fossils, *e.g*., *Byronia* Matthew, 1899, *Torellela* Linnarson, 1871, and *Annulitubus* Vinn *et al*., 2016 (Zhu *et al*., 2000; Vinn, 2006; Vinn *et al*., 2016a, b; Landing *et al*., 2018; Van Iten *et al*., 2019). *Sphenothallus* differs from *Cambrorhytium* Conway Morris & Robinson, 1988 in having a phosphatic rather than a purely organic composition. *Sphenothallus* differs from *Coleolus* Hall, 1879 in being phosphatic (Dernov, 2022).

Stratigraphic range. Cambrian–Carboniferous, Upper Triassic.

Sphenothallus sp. 1
(Figures 2A, C–E)

Material. Two poorly preserved specimens of the tube fragments in the black shale (IGS NASU-19/01a) and in a siderite concretion (IGS NASU-19/02).

Description. Specimen IGS NASU-19/01a (Figure 2A) is the best-preserved fossil in the core sample IGS NASU-19/01. The tube fragment of specimen IGS NASU-19/01a is 20 mm in length, slightly undulatory with a low rate of adapertural expansion (*c*. 3°), becoming thinner from the apertural end to the basal end. The maximum width of the tube (near the apertural end) is 1.1 mm, and the width of the basal part is 0.7 mm. The surface of the tube is smooth and does not bear any ornamentation. Two lateral tube thickenings, each measuring 0.15 mm wide, are clearly visible on all examined tube fragments. Specimen IGS NASU-19/02 (Figure 2C) is presented by the dark grey to almost black, 14-mm-long tube tube fragment and its 10-mm-long impression. The width of the tube (the diameter cannot be measured because the tube is crushed) is 5.5 mm and does not vary significantly. The tube margins are mostly straight. The tube wall has two lateral thickenings situated 180° apart and measuring 1 mm wide. The external surface of the tube is smooth. Only a few rounded and subconical holdfasts, measuring 0.8–1.1 mm in diameter (shown by arrows in Figure 2C and enlarged in Figure 2D), are present on the surface of the tube, and there is a mold of a single holdfast.

Remarks. The studied specimens were assigned to the genus *Sphenothallus* on the basis of the presence of two lateral thickenings and the broadly conical morphology of the holdfasts. *Sphenothallus* sp. 1 differs from *Sphenothallus* sp. 2, described below, in lacking very fine transverse ribs on the tube surface. The absence of fine ornamentation on the tube of *Sphenothallus* sp. 2 cannot be explained by a taphonomic artifact, since mudstone with this fossil was originated in depositional conditions of low current energy, which contributed to the preservation of delicate morphological details. For example, delicate ornamentation is always preserved on the shells of brachiopods, bivalves, gastropods, and cephalopods that occur together with *Sphenothallus* in the Mississippian sedimentary rocks of the Dnipro-Donets Depression.

Sphenothallus sp. 1 is similar to *Sphenothallus* cf. *carbonarius* (M'Coy, 1844) from the Upper Devonian Chagrin Shale in Ohio, USA (Feldmann *et al*., 1986; Neal & Hannibal, 2000) in having the tube surface smooth and in preserving the holdfast. Specimens of *Sphenothallus carbonarius* (M'Coy, 1844) figured by Wilson (1967: pl. 1, figs 8–16) show a faint transverse striation, which is absent on specimens IGS NASU-19/01 and IGS NASU-19/02. The fragmentary preservation and small amount of the material here studied do not allow

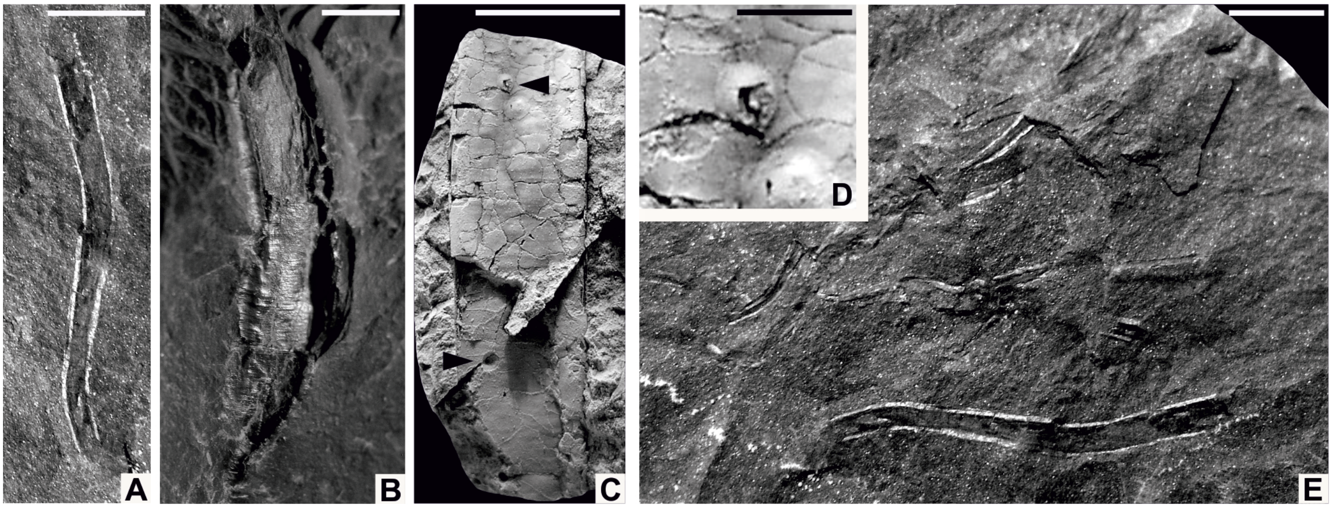

Figure 2. Remains of *Sphenothallus* from the Dnipro-Donets Depression: **A, C–E**, *Sphenothallus* sp. 1 (**A**, **E**, specimen IGS NASU-19/01; **C**, specimen IGS NASU-19/02, holdfasts are marked with black arrows; **D**, enlarged holdfast on the tube of specimen IGS NASU-19/02); **B**, *Sphenothallus* sp. 2 (specimen IGS NASU-19/03). Scale bars: A–C, E = 5 mm; and =1 mm.

a more detailed comparison of the described forms with *Sphenothallus carbonarius* (M'Coy, 1844).

Sphenothallus sp. 1 differs from *Sphenothallus ruedemanni* (Kobayashi, 1934) in having a more cylindrical tube form and smooth surface. Specimen IGS NASU-19/02 is somewhat similar to *Sphenothallus* aff. *longissimus* (Sowerby in Murchison, 1839) from the Late Ordovician of Estonia, figured by Vinn & Kirsimäe (2015: figs. 2A–C), but is noticeably smaller and lacks irregular perpendicular wrinkles on the tube surface.

The described specimens are also similar to *Enchostoma* sp. (=*Sphenothallus* sp.) from the Wewoka Formation of Oklahoma in the tube form, lack of ornamentation on the tube surface, and the low rate of adapertural expansion; however, the specimen figured by Girty (1915: pl. 5, fig. 6) lacks the holdfast.

Localities. Chernihiv and Poltava regions of Ukraine (for details, see the preceding section on Material and Methods).

Occurrence. Upper Viséan and ?Bashkirian (Carboniferous) of the Dnipro-Donets Depression, NE Ukraine.

Sphenothallus sp. 2
(Figure 2B)

Material. One poorly preserved specimen (IGS NASU-19/03) of a tube fragment on the black shale bedding plane.

Description. Specimen IGS NASU-19/03 (Figure 2B) consists of a small, crushed 24-mm-long, weakly undulatory tube fragment with a low rate of adapertural expansion; the tube fragment becomes thinner from the apertural end to the basal end. The width of the tube is 4.7 mm. The surface of the tube exhibits thin transverse ribs measuring 0.15 mm thick. Two lateral tube thickenings, each measuring 0.8 mm wide, are clearly visible on the tube fragment.

Remarks. See the "Remarks" section in the description of *Sphenothallus* sp. 1.

Locality. Poltava Region of Ukraine (for details, see the preceding section on Material and Methods).

Occurrence. Upper Viséan of the Dnipro-Dontes Depression, NE Ukraine.

DISCUSSION

The three valid Carboniferous species of *Sphenothallus* noted above in the introductory section differ very slightly in their gross morphology. The detailed original diagnoses of these species are presented below.

Sphenothallus carbonarius (M'Coy, 1844): "Tube small and narrow, flexuous, phosphatic with two lateral longitudinal thickenings and an oval cross-section in the proximal stages, but as the breadth increases the tube becomes flatter and strap-like and probably concavo-convex in the mature part; initial stage of the tube with holdfast. Well-preserved specimens show a faint transverse striation" (after M'Coy, 1844; Wilson, 1967).

Sphenothallus bicarinatus (Girty, 1911): "The longest specimens measure over 30 mm, have subparallel sides, and are apparently incomplete at both ends. The largest have a diameter of only 1.25 mm. They differ in appearance according to their position in the rock, two opposite sides being, as it were, stiffened and reinforced into carina and the intermediate membrane being more tenuous and flexible. In one position the two sides are sharply defined by slightly raised ridges, the intervening connective tissue being flattened and less substantial. When turned on the side they show a central carina with another corresponding to it concealed in the rock. In this position the width, as represented by our specimens, is narrower than in the other" (after Girty, 1911: p. 28).

Sphenothallus stubblefieldi Schmidt & Teichmüller, 1956: "Tube small and narrow, flexuous, smooth, phosphatic with two lateral longitudinal thickenings and an oval cross-section" (after Schmidt & Teichmüller, 1956, 1958).

The problem of whether the previous three species are mutually synonymous could not be resolved in the present study. Therefore, the specific identity of the forms here described from Ukraine could not be determined. Paleoecology and taphonomy cannot be interpreted in detail here since the studied specimens belong to a rather old collection of samples obtained from geologists involved in oil and gas exploration. Apparently, like certain other representatives of the genus *Sphenothallus*, the specimens from the Dnipro-Donets Depression led an epifaunal and gregarious lifestyle, preferring relatively deep, basinal environments with slow sedimentation rates, low current energy, dysaerobic conditions (Lerner & Lucas, 2011).

FINAL REMARKS

Two unnamed species of the medusozoan cnidarian *Sphenothallus* occur in dark gray, basinal shales of the Late Mississippian and Early Pennsylvanian age in modern northeastern Ukraine. These sediments were deposited in relatively deep, dysaerobic marine water in which sedimentation rates were low. The present discovery expands our knowledge of the geographic distribution of these animals and provides additional evidence suggesting that *Sphenothallus* was an opportunistic animal capable of withstanding oxygen stress.

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