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First Report of *Sphenothallus* Hall (Cnidaria, Medusozoa) from the Mesozoic Erathem (Upper Triassic, Slovenia)

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Introduction

Sphenothallus Hall, 1847, one of the most widely distributed and longest ranging genera in the fossil record, has been documented from all systems of the Paleozoic Erathem except the Permian (Table 1), although it has been stated (e.g., Choi, 1990; Bolton, 1994; Fatka et al., 2012) that the genus also occurs in that system. At present the first appearance of this epibenthic, polypoid medusozoan cnidarian lies in Cambrian Stage 3, while the previously known youngest occurrences are in the Pennsylvanian System. *Sphenothallus* has been found in numerous formations on all continents except Australia and Antarctica. It occurs in a variety of marine facies ranging from shallow nearshore to deep offshore and has even been found in strata of coastal lacustrine origin, probably as an allochthonous element (Lerner and Lucas, 2011). Many of the rock units known to contain *Sphenothallus* also contain conulariids (Table 1), an extinct group of marine scyphozoans that may have been closely related to *Sphenothallus* (Van Iten et al., 1992, 1996). Van Iten et al. (1992) interpreted *Sphenothallus* as a medusozoan cnidarian of uncertain class-level affinities, but later Dzik et al. (2017) documented internal peridermal structures that may be homologous to similar features in the periderm of coronate scyphozoans (see for example illustrations in Van Iten, 1992, and Van Iten et al., 1996).

The present article describes multiple, very well-preserved specimens of *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) from limestone strata of early Late Triassic (late Carnian) age in the Julian Alps of northwest Slovenia. Some of these specimens were originally described under the name *Valvasoria carniolica* Kolar-Jurkovšek and Jurkovšek, 1997, which was interpreted as a tubiculous worm of possible nematode or sipunculid affinities (see also Hitij et al., 2019). Thus, this is the first report of *Sphenothallus* from the Mesozoic Erathem. Furthermore, *Sphenothallus* is now established as a long-ranging medusozoan cnidarian, which, together with conulariids, survived the End Permian Mass Extinction Event (MacLeod, 2013).

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Geological setting

The studied *Sphenothallus* specimens were collected from thin, gray, laminated lime mudstones in the Kozja dnina Member of the Martuljek Limestone (early Late Triassic, late Carnian) in the northeast Julian Alps (Vrata Valley) of northwest Slovenia (Fig. 1). The late Carnian (Tuvalian) age of the section that yielded the specimens is based on conodont assemblages (*Quadralella polygnathiformis* Zone; Kolar-Jurkovšek, 1991). The section at Kozja dnina is ∼80 m thick and represents a deep water paleoenvironment (Bitner et al., 2010). The strata were deposited in an interplatform basin, where anoxic conditions and rapid sedimentation enabled exceptional preservation of both invertebrate and vertebrate fossils (Celarc and Kolar-Jurkovšek, 2008). In addition to *Sphenothallus*, the Kozja dnina limestones also contain bivalves, brachiopods, echinoids, crinoids, asteroids, ammonites, belemnites, scleractinian corals, shrimp, lobsters, thylacocephalans, and fishes (Hitij et al., 2019; Gašparič et al., 2020).

Material and methods

The present study is based on direct examination of 31 specimens of *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) from the Kozja dnina Member of the Martuljek Limestone. All specimens occur on exposed bedding planes, their preserved periderm appearing light to dark brown on the light gray weathered limestone, in some cases with a blueish hue resulting from vivianitization. Specimens were examined and photographed using reflected light and scanning electron microscopy (secondary electron mode). Material photographed under reflected light was whitened with ammonium chloride sublimate. Photographs were taken with a millimetric scale bar using a Nikon Z 6II digital camera equipped with a NIKKOR Z MC 105mm f/2.8 VR S lens. Photographs were edited in Photoshop CS6, and figures containing light photographs were assembled in CorelDRAW X8. Scanning electron microscopy was conducted using a JEOL JSM-649OLV. Finally, the elemental composition of the periderm of one of the specimens (T-1287) was determined using an Oxford INCA Energy 350 EDS under the following operating conditions: chamber vacuum

Table 1. Selected documented occurrences of *Sphenothallus* Hall, 1847, in the Phanerozoic rock record. Asterisk next to a formation or member name indicates that the unit also yields conulariids.

System	Stage(s) or Series	Formation(s)	Locality(ies)	Reference(s)
Cambrian	Stage 3	Guojiaba, Xiannudong	China (Shaanxi Province)	Li et al., 2004
	Stage 3	Niutitang	China (Hunan and Guizhou provinces)	Peng et al., 2005; Muscente and Xiao, 2015
	Stage 3	Balkasandstein	Denmark	Troppenz, 2020
	Stages 3–4	Shipai, Shuijingtuo	China (Hubei Province)	Muscente and Xiao, 2015; Chang et al., 2018
	Stage 4	Kaili	China (Anhui Province)	Zhao et al., 1999; Zhu et al., 2000; Peng et al., 2005
	Stage 4	Harkless	USA (Nevada)	Skovsted and Holmer, 2006
	Wuliuan	Stephen	Canada (British Columbia)	Van Iten et al., 2002
	Wuliuan	Jince	Czech Republic	Fatka et al., 2012
	Wuliuan	Buchava Skryje Mbr.	Czech Republic	Fatka and Kraft, 2013
Ordovician	Tremadocian	Dumugol	Korea	Choi, 1990
	Tremadocian–Floian	Fezouata Shale*	Morocco	Van Iten et al., 2016a
	Floian	Tonggao *	China (Hubei Province)	Van Iten et al., 2013
	Floian	Fenxiang*	China (Hubei Province)	Baliński and Sun, 2015; Dzik et al., 2017
	Floian–Dapingian	Klabava*	Czech Republic	Bruthansová and Van Iten, 2020
	Sandbian	Zahořany*	Czech Republic	Bruthansová and Van Iten, 2020
	Sandbian	Viivikonna*	Estonia	Vinn and Kirsimäe, 2015
	Sandbian–Katian	Dillsboro*	USA (Indiana)	Bodenbender et al., 1989
	Katian	Lindsay Collingwood Mbr.*	Canada (Ontario)	Bolton, 1994
	Katian	Utica Shale*	Canada (Quebec)	Bolton, 1994
	Katian	Maquoketa Elgin* and Brainard* mbrs.	USA (Iowa and Minnesota)	Van Iten et al., 1996, 2005
Silurian	Rhuddanian	Lung-Machi	China (Guizhou Province)	Yi et al., 2003
	Telychian	Brandon Bridge	USA (Wisconsin)	Miller et al., 2022
	Llandovery	Cape Schuchert	Greenland	Peel, 2021
Devonian	Emsian	Hunsrück Slate*	Germany	Fauchald et al., 1986; Südkamp, 2017
	(multiple)	(multiple)	USA (multiple states)	Mason and Yochelson, 1985
	Pragian–Emsian	Ponta Grossa Shale Jaguariaíva Mbr.*	Brazil (Paraná State)	Van Iten et al., 2019
	Famennian	Chagrin Shale*	USA (Ohio)	Feldmann et al., 1986; Neal and Hannibal, 2000
Mississippian	Serpukhovian	Heath Bear Gulch Mbr.*	USA (Montana)	Van Iten et al., 1992
	Serpukhovian	Gurovo Dashkovko Mbr.*	Russia (Moscow Basin)	Van Iten et al., 2022
	(multiple)	(multiple)	USA (multiple states)	Mason and Yochelson, 1985
Pennsylvanian	Kazimovian	Atrasado Tinajas Mbr.	USA (New Mexico)	Lerner and Lucas, 2005, 2011
	(multiple)	(multiple)	USA (multiple states)	Mason and Yochelson, 1985
	(multiple)	(multiple)	Belgium, France, Germany, Netherlands	Schmidt and Teichmüller, 1956, 1958
Triassic	Carnian	Martuljek Limestone Kozja dnina Mbr.	Slovenia	This paper

20 Pa, accelerating voltage 20 kV, spot size 48 µm, working distance 10 mm, and analysis time 60 seconds.

Repositories and institutional abbreviations.—BJ = Paleontological collection of Jurkovšek, Dol pri Lubljani, Slovenia. T = Paleontological collection of Tomaž Hitij and Jure Žalohar, Godič, Slovenia. All collections are registered at the Slovenian Museum of Natural History in Ljubljana.

Systematic paleontology

Phylum Cnidaria Verrill, 1865
Subphylum Medusozoa Peterson, 1979
Class, Order, Family uncertain
Genus *Sphenothallus* Hall, 1847

Type species.—*Sphenothallus angustifolius* Hall, 1847, originally described from the Upper Ordovician of eastern New York State, USA.

Sphenothallus carniolica (Kolar-Jurkovšek and Jurkovšek, 1997)
Figures 3–5

1997 *Valvasoria carniolica* Kolar-Jurkovšek and Jurkovšek, p. 1, pl. 1, figs. 1–4.
2019 *Valvasoria carniolica*; Hitij et al., p. 21, figs. 16, 17.

Holotype.—BJ1286 (originally designated as the holotype of *Valvasoria carniolica* Kolar-Jurkovšek and Jurkovšek, 1997; currently reposited in the collection of Bogdan Jurkovšek).

Paratypes.—BJ1287, BJ1419 (originally designated as paratypes of *Valvasoria carniolica*; currently reposited in the collection of Bogdan Jurkovšek).

Diagnosis.—Peridermal tube very gently tapered (angle of expansion mostly <2°), non-branching, lacking regular transverse annulations.

Occurrence.—Thin, gray, laminated lime mudstones in the Kozja dnina Member of the Martuljek Limestone (early Late Triassic, late Carnian, Tuvalian; *Paragondolella polygnathiformis* conodont Zone) in the Vrata Valley in the northeast Julian Alps, northwest Slovenia. The geographic coordinates of the fossil locality are Lat. 46°24′08.1″N, Long. 13°50′46.2″E.

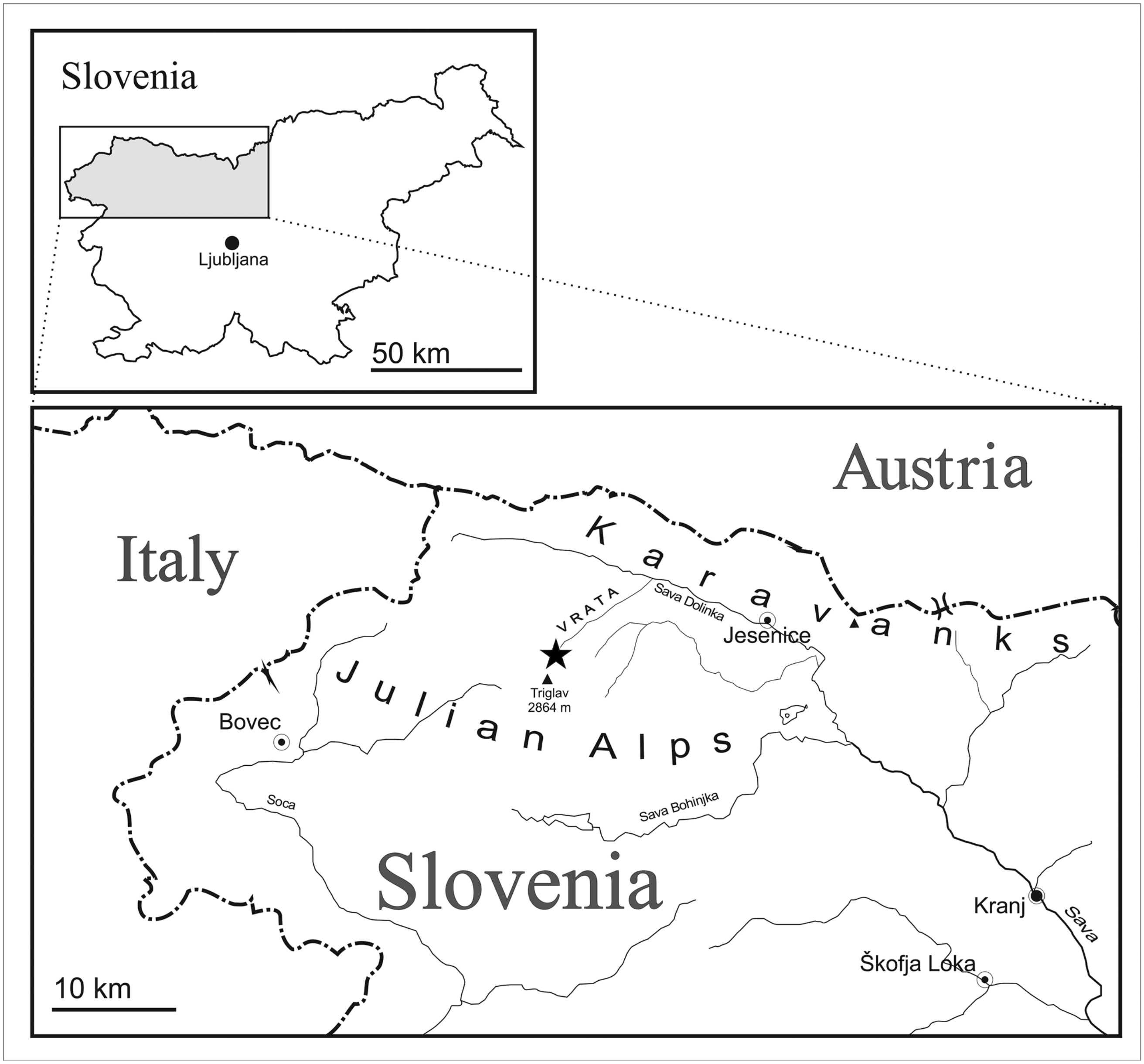

Figure 1. Simplified geographical map of northwest Slovenia. The location of Kozja dnina in the Vrata Valley is marked by a star (figure adapted from Bitner et al., 2010).

Description.—Partial to nearly complete, compressed specimens lying parallel to bedding and ranging up to 129.5 mm in length and 5.5 mm in width. Specimens consist of one or more portions of the slender, originally sub-elliptical (transversely) main tube or of nearly the entire periderm, including the sub-conical attachment disc, although without the basal membrane. Attachment disc measures up to ∼3.1 mm in diameter. Apertural margin not preserved; terminal schott (apical wall) absent. Main tube very gently tapered (mostly <2°) in the plane of the well-developed pair of oppositely situated, longitudinal thickenings, variably curved parallel to bedding, in some cases with the degree of curvature increasing toward the apical end. Relatively thin periderm between the longitudinal thickenings missing or, where present, exhibiting coarse, irregular, transverse to oblique wrinkles. Regular transverse annulations absent. Longitudinal thickenings terminate or thin near the apertural end of the main tube. Skeletal material phosphatic, very finely lamellar, light to dark brown or dark bluish gray, with exfoliated lamellae in some specimens exhibiting possible "plywood [micro]structure" (Vinn and Mironenko, 2021). Some specimens exhibit minute, shallow, sub-circular to sub-elliptical pores or pits ranging from ∼2–4 µm in diameter.

Additional material.—BJ2505 (currently reposited in the collection of Bogdan Jurkovšek); T-1256, T-1257, T-1270–T-1287 (currently reposited in the collection of Tomaž Hitij and Jure Žalohar).

Remarks.—The principal diagnostic feature of *Sphenothallus*, namely the pair of longitudinal thickenings situated at the end points of the major diameter of the subelliptical main tube, is

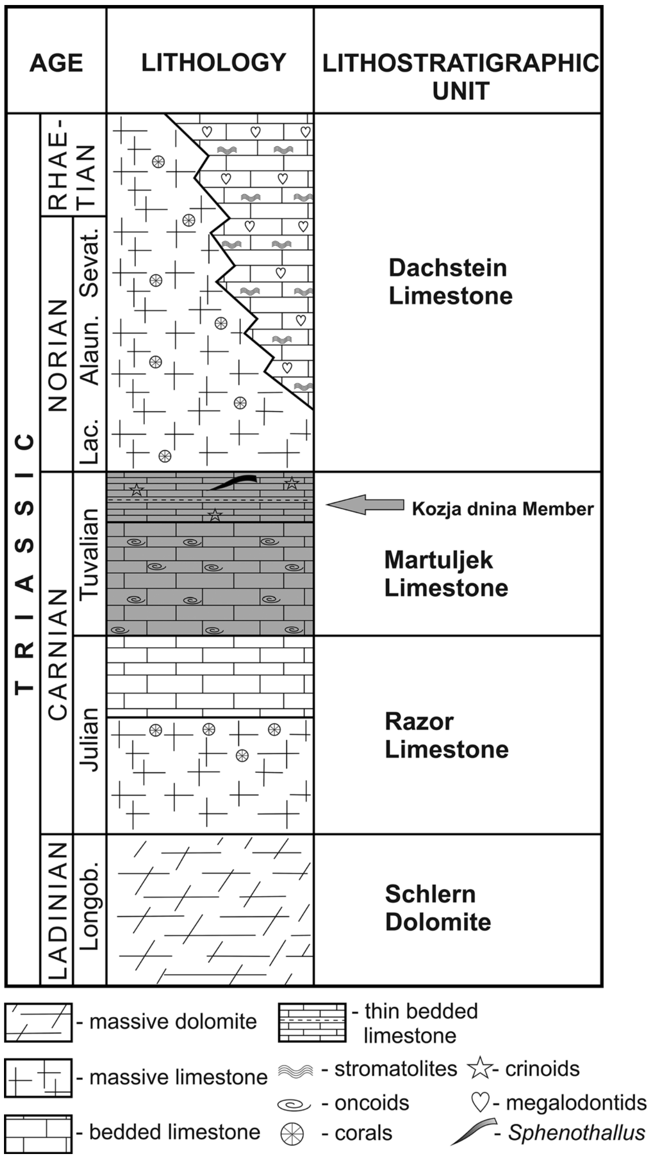

Figure 2. Lithostratigraphy of the Tuvalian section with platy limestones yielding *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) (arrow) at Kozja dnina (figure adapted from Celarc and Kolar-Jurkovšek, 2008). Norian stage subdivisions are abbreviated as: Lac. = Lacian; Alaun. = Alaunian; Sevat. = Sevatian.

well developed in the Slovenian material (Figs. 3.1–3.3, 3.5, 4.1–4.3, 5.1–5.4, 5.8). As in *Sphenothallus* from Paleozoic formations, compression of the Slovenian specimens perpendicular to bedding has caused the longitudinal thickenings to form berm-like elevations rising above the thinner, deformed skeletal wall between them, which in some cases (Fig. 5.8) is now absent. Also well displayed in the Slovenian material is the characteristic, parallel lamellar microstructure (Figs. 4.8, 5.5, 5.6), which is commonly exfoliated. Lamellae in one specimen appear to exhibit "plywood [micro]structure" (Fig. 5.5, 5.6), discovered by Vinn and Mironenko (2021, fig. 2C, D) in material from the Upper Mississippian of central Russia. A somewhat similar microstructure is present in the medusozoan *Torellella* Holm, 1893, from the upper Cambrian of Estonia (Vinn, 2006, 2022). The presence of calcium phosphate (apatite), which constitutes the bulk of most Paleozoic specimens, is corroborated both by the brown to blue-gray color of the specimens and by the results of EDS analysis (Fig. 6), which yielded strong spectral peaks for Ca and P.

Turning to other characters, the very low rate of taper of the main tube of the Slovenian specimens is similar to that of *S. angustifolius* from the Upper Ordovician of Ontario and Quebec, Canada (see for example Bolton, 1994, pls. 1.1–1.3) and *S. sica* Clarke, 1913, from the Lower Devonian Ponta Grossa Shale of Brazil (see for example Van Iten et al., 2019, fig. 4). The size of the attachment disc (Figs. 3.1, 3.2, 3.4, 3.5, 4.1–4.4, 4.6, 4.7, 5.1, 5.2), both absolute and in proportion to the size of the main tube, matches closely that of the attachment disc of *Sphenothallus* sp. from the Bear Gulch Member of the Upper Mississippian Heath Formation of Montana, western USA (see Van Iten et al., 1992, fig. 1). Interestingly, specimens preserving both the attachment disc and the long slender tube above it may be attached to hard biological substrates (see for example Van Iten et al., 2019, fig. 6), or, like the Slovenian specimens and the Bear Gulch material referred to in the preceding sentence, they may be unattached, suggesting that their original substrate may have been plant or other organic matter susceptible to rapid decay. Finally, smooth curvature of the main tube, with the degree of curvature commonly decreasing in the direction of the apertural end (Figs. 3.2, 4.1, 4.2, 4.6, 5.3, 5.4, 5.6), is a feature exhibited by many Paleozoic specimens (see for example Van Iten et al., 1996, pl. 2.1), as are thinning of the longitudinal thickenings in the vicinity of the aperture (Figs. 3.1, 3.3, 5.4) and the absence of well-defined annulation or other ornament (Fig. 4.5).

A noteworthy additional feature, previously documented in *Sphenothallus* cf. *S. angustifolius* from the Upper Mississippian of central Russia (Vinn and Mironenko, 2021, fig. 2f), is the presence in the main tube of some of the Slovenian specimens of microscopic, sub-circular to sub-elliptical pores or pits (Fig. 5.7), originally detected in specimen BJ1287 by Kolar-Jurkovšek and Jurkovšek (1997, figs. 2, 3). These shallow perforations are similar in size, shape, areal density, and pattern of distribution to the microscopic circular pores, or micropores, of conulariids (see Van Iten et al., 2005, 2006a, b, 2022, and references cited therein). Conulariid micropores have been compared with microscopic borings and bioclaustrations, and they have been interpreted as primary anatomical features. If the latter hypothesis is true, then the presence of these features in conulariids and *Sphenothallus* may provide additional support for the hypothesis (e.g., Van Iten et al., 1996) that the skeletons of these two taxa are mutually homologous.

Concluding remarks

Sphenothallus Hall, 1847, an extinct genus of medusozoan cnidarians, is now known from the lower Upper Triassic of northwest Slovenia (Julian Alps). Moreover, the well-preserved specimens of *S. carniolica* from Slovenia are the only documented representatives of the genus from the Mesozoic Erathem. The present discovery extends the known age range of *Sphenothallus* by ca. 80 million years, from the Kazimovian to the late Carnian, and thus across the critical Permian-Triassic boundary.

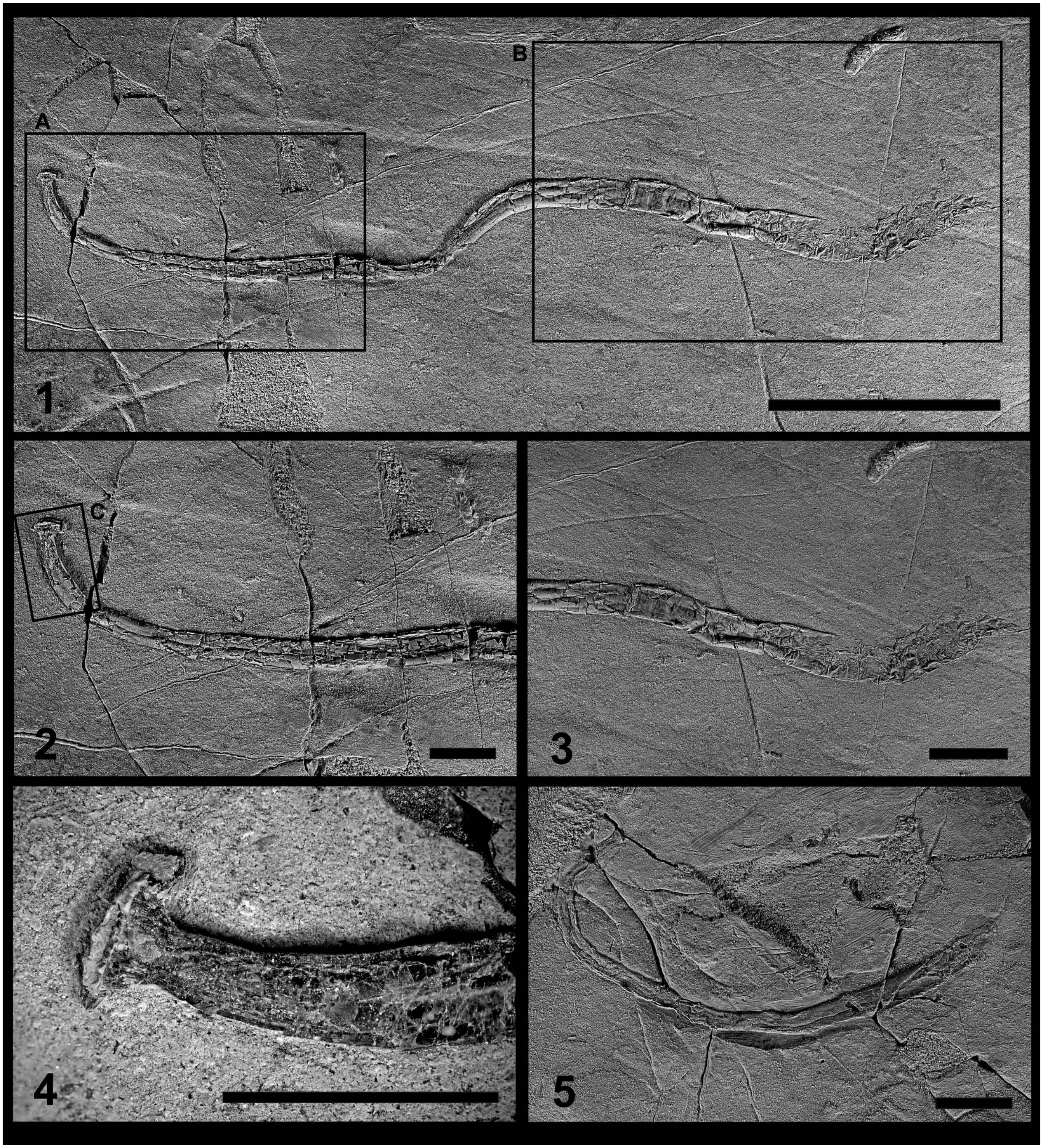

Figure 3. *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) from the Late Triassic (late Carnian) Kozja dnina Member of the Martuljek Limestone of northwest Slovenia (Vrata Valley). (**1–4**) BJ1286, the holotype and most complete specimen: (**1**) side view of the entire specimen, which preserves both the apical holdfast (left end of the specimen) and the apertural region of the main tube (right end of the specimen); (**2**) detail of the area in box (A) in (**1**), showing the apical region with berm-like marginal thickenings; (**3**) detail of the area in box (B) in (**1**), showing the heavily crumpled, relatively thin apertural region; (**4**) detail of the area in box (C) in (**2**), highlighting the sub-conical apical holdfast; (**5**) BJ1419, paratype, a nearly complete specimen with partially preserved apical holdfast. Scale bars = 30 mm (**1**) and 10 mm (**2–5**).

Additionally, since *Sphenothallus* has not yet been documented from any part of the Permian System, it may be a Lazarus taxon (Jablonski, 1986). Nevertheless, we predict that the existence of *Sphenothallus* of Permian age, previously only asserted, will be confirmed and that additional discoveries of Triassic and maybe even younger *Sphenothallus* will be made, based in part on the ability of *Sphenothallus* to survive the most severe crisis in the history of life during the Phanerozoic Eon. Finally, given the

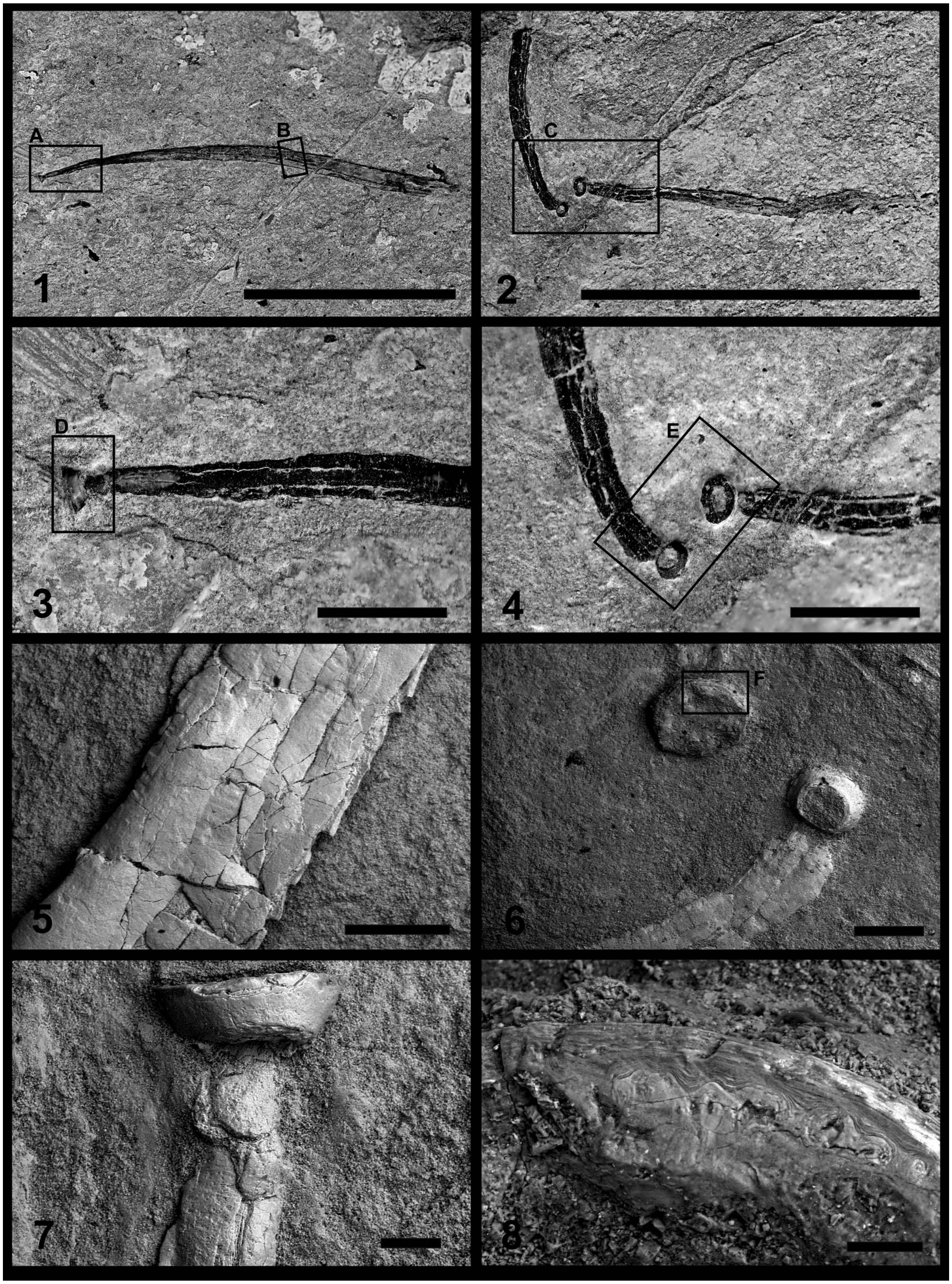

Figure 4. *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) from the Late Triassic (late Carnian) Kozja dnina Member of the Martuljek Limestone of northwest Slovenia (Vrata Valley). (**1**) T-1277, mostly complete specimen preserving the apical holdfast; (**2**) T-1270, two nearly contiguous specimens, both preserving the upper portion of the apical holdfast (basal membrane missing); (**3**) detail of the area in box (A) in (**1**), highlighting the apical region; (**4**) detail of the area in box (C) in (**2**), showing the apical regions of the two nearly contiguous specimens; (**5**, **7**) scanning electron photomicrographs of T-1277: (**5**) detail of the area in box (B) in (**1**), showing the non-annulated external surface of the main tube; (**7**) detail of the area in box (D) in (**3**), showing the apicalmost portion of the periderm (**7**); (**6**, **8**) scanning electron photomicrographs of T-1270: (**6**) detail of the area in box (E) in (**4**), showing the apicalmost portions of the specimens; (**8**) detail of the area in box (F) in (**6**), showing the wavy laminated microstructure of one the two holdfasts in transverse cross section (**8**). Scale bars = 10 mm (**1**, **2**), 1 mm (**3**, **4**), 500 µm (**5**, **6**), 100 µm (**7**), and 50 µm (**8**).

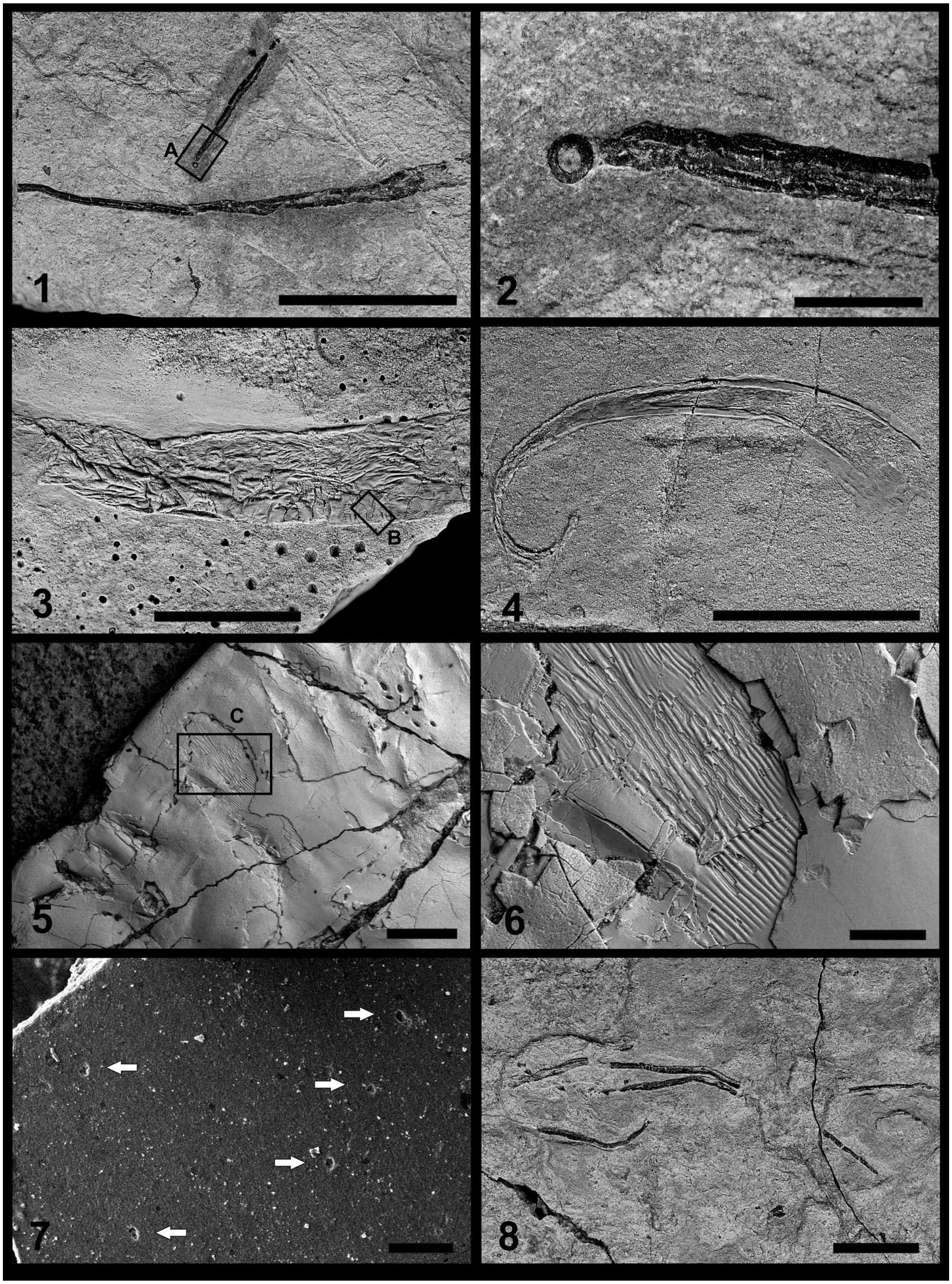

Figure 5. *Sphenothallus carniolica* (Kolar-Jurkovšek and Jurkovšek, 1997) from the Late Triassic (late Carnian) Kozja dnina Member of the Martuljek Limestone of northwest Slovenia (Vrata Valley). (**1**) T-1273, two associated specimens, the shorter one of which preserves the apical holdfast; (**2**) detail of the box (A) in (**1**), highlighting the apical holdfast and the marginal thickenings, which are slightly elevated above the thinner periderm between them; (**3**) T-1257, portion of the main tube of a nearly complete specimen exhibiting pervasive irregular wrinkling of the thin periderm between the longitudinal thickenings; (**4**) T-1256, nearly complete specimen exhibiting pronounced curvature of the main tube in the apical region (left) and pervasive wrinkling of the thin periderm between the robust longitudinal thickenings (right); (**5**) detail (scanning electron micrograph) of the box (B) in (**3**), showing the absence of regular annulation of the main tube as well as areas (central part of the field of view) of possible "plywood [micro]structure" (Vinn and Mironenko, 2021); (**6**) detail (scanning electron micrograph) of the box (C) in (**5**), showing one of the areas of possible "plywood [micro]structure" (Vinn and Mironenko, 2021); (**7**) scanning electron micrograph of BJ1419, showing multiple, sub-circular micropores (arrows) on the surface of the periderm; (**8**) T-1271, assemblage of at least four specimens consisting entirely or predominantly of one or both longitudinal thickenings. Scale bars = 10 mm (**1**, **3**, **4**, **6**, **8**), 1 mm (**2**), 500 μm (**5**), and 20 μm (**7**).

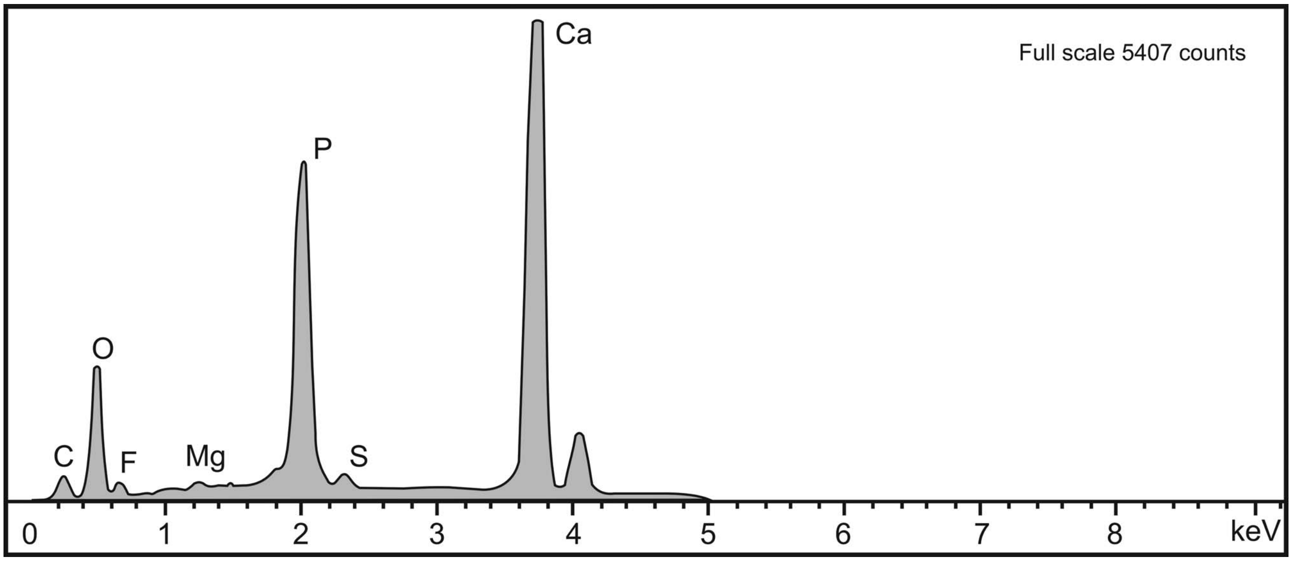

Figure 6. EDS spectrum of specimen T-1287, corroborating the presence of calcium phosphate in the periderm.

presence of conulariids, which are commonly associated with *Sphenothallus*, in strata of terminal Ediacaran age (Van Iten et al., 2016b; Leme et al., 2022), we would not be surprised if the first appearance of *Sphenothallus* were extended downward into that system.

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Declaration of competing interests

The authors declare none.

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