On the enigma of *Palaenigma wrangeli* (Schmidt), a conulariid with a partly non-mineralized skeleton

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Palaenigma wrangeli (Schmidt) is a finger-sized fossil with a tetraradiate conical skeleton; it occurs as a rare component in fossiliferous Upper Ordovician strata of the eastern Baltic Basin and is known exclusively from north Estonia. The systematic affinities and palaeoecology of *P. wrangeli* remained questionable. Here, the available specimens of *P. wrangeli* have been reexamined using environmental scanning electron microscopy and x-ray computed tomography. Additionally, the elemental composition of the skeletal elements has been checked using energy dispersive X-ray spectroscopy. The resulting 2D-, and 3D-scans reveal that *P. wrangeli* consists of an alternation of distinct calcium phosphate (apatite) lamellae and originally organic-rich inter-layers. The lamellae form four semicircular marginal pillars, which are connected by irregularly spaced transverse diaphragms. Marginally, the diaphragms and pillar lamellae are not connected to each other and thus do not form a closed conch structure. A non-mineralized or poorly mineralized external conch probably existed originally in *P. wrangeli* but is not preserved in the available material. *P. wrangeli* often co-occurs with conulariids in fossil-rich limestone with mudstone – wackestone lithologies. Based on the new data, P. wrangeli can be best interpreted as a poorly mineralized conulariinid with a mud-sticking life habit. Here the new conulariinid family Palaenigmaidae fam. nov. is proposed as the monotypic taxon for *P. wrangeli*.

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Abstract

Palaenigma wrangeli (Schmidt) is a finger-sized fossil with a tetraradiate conical skeleton; it occurs as a rare component in fossiliferous Upper Ordovician strata of the eastern Baltic Basin and is known exclusively from north Estonia. The systematic affinities and palaeoecology of *P. wrangeli* remained questionable. Here, the available specimens of *P. wrangeli* have been reexamined using environmental scanning electron microscopy and x-ray computed tomography. Additionally, the elemental composition of the skeletal elements has been checked using energy dispersive X-ray spectroscopy. The resulting 2D-, and 3D-scans reveal that *P. wrangeli* consists of an alternation of distinct calcium phosphate (apatite) lamellae and originally organic-rich inter-layers. The lamellae form four semicircular marginal pillars, which are connected by irregularly spaced transverse diaphragms. Marginally, the diaphragms and pillar lamellae are not connected to each other and thus do not form a closed conch structure. A non-mineralized or poorly mineralized external conch probably existed originally in *P. wrangeli* but is not preserved in the available material. *P. wrangeli* often co-occurs with conulariids in fossil-rich limestone with mudstone – wackestone lithologies. Based on the new data, P. wrangeli can be best interpreted as a poorly mineralized conulariinid with a mud-sticking life habit. Here the new conulariinid family Palaenigmaidae fam. nov. is proposed as the monotypic taxon for *P. wrangeli*.

Introduction

The fossil *Palaenigma wrangeli* (Schmidt, 1874) captivates. It is small, less than a small finger in diameter and no more than a couple of centimeters long. *P. wrangeli* has a beautiful tetraradiate symmetry with four, strange horn-like spines or pillars at each corner, and it consists of a shiny, dark-brown calcium phosphate, which cannot be overlooked on a freshly broken Ordovician limestone.

The species name refers to Wilhelm F. Baron von Wrangell (1831–1894) (son of the famous seaman Ferdinand von Wrangel), who found this fossil not far from his manor house when he was a young man only to urge twenty years later the Geologist Friedrich K. Schmidt (1832–1908) to solve its mystery. In his original description of the fossil, Schmidt (1874) reported the difficulties in finding more material. It took him two years and hours of focused searching to find another good specimen in a small quarry, where Wrangell guided him and his younger Swedish colleague Jonas. G. O. Linnarson (1841–1881). The quarry exposed the Lyckholmsche Schicht (corresponding to the Nabala and Vormsi Regional stages) and, according to Schmidt (1874), was very rich in conulariids. The dark phosphatic shell of conulariids and the skeleton of *P. wrangeli* stand out in the greenish-pale limestone, and if *P. wrangeli* were abundant, it would have been easy to be found by the experienced and dedicated fossil hunters.

P. wrangeli is generally a rare fossil known exclusively from Estonia, and from Pleistocene erratic blocks from the Åland Islands, Finland and Uppland, Sweden (Holm, 1893). In the palaeontological collections of Estonia only seven specimens have been accumulated until now. The specimen found by Wrangell and the four or so, original specimens collected by Schmidt and Linnarson are unfortunately lost. Two specimens, probably collected by Linnarson, are in the collections of the Naturhistorisk Riksmuseet Stockholm (Sweden). All come from north Estonian light-coloured Upper Ordovician limestone, which is generally poor in skeletal intraclasts (Fig. 1).

Schmidt (1874) couldn't solve the mystery of *Palaenigma*, for which he created the separate genus *Tetradium*, a name that was already preoccupied by a coral (see Walcott, 1886). He speculated that it could be an operculum of a conulariid. Walcott (1886, p. 224) compared it with the Cambrian calcitic polyplacophoran *Mattheva* Walcott. Before, Lindström (1884, p. 41), in his opus magnum on Silurian gastropods of Gotland, excluded any relation with mollusks and curiously suggested that it might be a conulariid infected by a parasitic fungus. Later, Sinclair (1952) placed *Palaenigma* without comment into the Conulariinae, a family of the Conulariida. The conulariid affinities of *P. wrangeli* also appeared unquestionable for Brood (1995), who briefly described the species and interpreted it as a basal part of *Conularia* Sowerby (Brood, 1995). The genus, however, does not appear in the Treatise of Invertebrate Palaeontology (Moore & Harrington, 1956) and it was not included in the review and cladistic analysis of the Conulariinae carried out by De Moraes Leme et al. (2008).

New finds from a small quarry in central Estonia exposing the Saunja Formation (Nabala Regional Stage) give an opportunity to take the mysterious species under a new scrutiny using modern analytical techniques. Here we describe the new material and review existing specimens available from the Estonian geoscience data platform SARV), and the ~~Nauturhistorisk~~ Riskmuseet Stockholm (NRM). SARV unites the large palaeontological collections from Estonia, housed at the Department of Geology at Tallinn University of Technology (GIT), the Natural History Museum, University of Tartu, and the Estonian Museum of Natural History.

Methods

The specimens were investigated with a GE phoenix v|tome|x s X-ray computed tomography (CT) device at the Geological Survey of Finland in Espoo, Finland. The samples were imaged using an accelerating voltage of 80-100 kV and a tube current of 120-220 μA, for a tube power of 12-22 W. Tube power was kept low enough to avoid spot size – related blurring for the obtained resolutions of 12-20 μm. 0.1 mm of Cu was used as a beam filter in most scans. 2200-2500 angle steps were used and at each angle the detector waited for a single exposure time and then took an average over three exposures, with the single exposure time varying between 500-1000 ms. This resulted in total scan times of 73-167 minutes. The obtained projections were reconstructed using GE phoenix datos|x and investigated using ThermoFisher PerGeos 2020.2. The specimens have also been subjected for microstructural observation using the environmental scanning electron microscope (ESEM) FEI Quanta 250 housed at the Institute of Earth Sciences in Sosnowiec, Poland. The specimens have been inspected in uncoated states in low vacuum conditions using back-scattered (BSE) imaging. Both transverse and longitudinal sections of the specimens have been investigated. The elemental composition of building structures and layers have been checked using an energy dispersive X-ray spectroscopy (EDS) detector. ESEM and CT images have been graphically improved by adjusting whole image Gamma and Contrast levels using Affinity Photo Version 1.9.2 graphical software. Herein, a few descriptive terms are used, which are mainly borrowed from the literature about conulariids: Periderm denotes the exoskeleton of conulariids. Carinae are broad, internal thickenings of the periderm that can be situated on the sides of the periderm or as keel-like, continuous thickenings at the corners of the periderm. In many conulariids there are multiple kinds of internal thickenings, collectively assigned by Bischoff (1978) and Van Iten (1992) to 11 types of internal midline (interradial) structures and two types of internal corner (perradial) structures. Septa are longitudinal walls, keels, and deep ridges in the interior of the periderm positioned at the midline. Diaphragms are horizontal truncations of the periderm well above the apex. At the position of a diaphragm the periderm tapers to an imperforate, usually adapically convex transverse wall, sometimes also called the “apical wall”, or “schott” Van Iten (1991).

The compilation of conulariid specimens is based on a search in the SARV database (accessed 08.04.2021, http://geocollections.info/specimen?specimen_number_1=1&specimen_number=&collection_id_1=1&collection_id=&classification_1=2&classification=&taxon_1=2&taxon=conulari&name_geology_1=1&name_geology=&country_1=1&country=&locality_1=1&locality=&stratigraphy_1=11&stratigraphy=Haljala%20Stage&id_1=5&id=&depth_since_1=12&depth_since=&depth_to_1=13&depth_to=&agent_1=1&agent=&reference_1=1&reference=&original_type_1=1&original_type=&part_1=1&part=&date_taken_since_1=12&date_taken_since=&date_taken_to_1=13&date_taken_to=&dbs%5B%5D=1&dbs%5B%5D=2&dbs%5B%5D=3&currentTable=specimen&maxSize=5&page=1&paginateBy=25&sort=locality__locality_en&sortdir=DESC)

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Geological setting

All specimens of *P. wrangeli* described herein have been collected from localities in north Estonia, exposing Upper Ordovician strata either in natural outcrops or in drill cores (Fig. 1A). The sediments of north Estonia are tectonically nearly undisturbed and palaeogeographically represent the eastern part of the Baltic Palaeobasin of the Baltica Palaeocontinent (Männil, 1966; Jaanusson, 1979; Nestor and Einasto, 1997). During the Late Ordovician the sedimentary deposition in north Estonia was dominated by limestone and marlstone in temperate to tropical marine settings (Cocks and Torsvik, 2005; Dronov and Rozhnov, 2007). The area comprises the North Estonian Facies Belt or North Estonian Shelf which, toward the south, grades into the Livonian Basin (Jaanusson 1979; Nestor & Einasto, 1997, Fig. 1B). The sediments of the North Estonian Shelf are predominantly neritic to shallow marine and individual sedimentary packages are locally divided by long depositional hiati and partially by erosional horizons (Raukas and Teedumäe, 1997). A well-established regional chronostratigraphic, lithostratigraphic and biostratigraphic scheme allows for high resolution correlation of the north Estonian Upper Ordovician sediments (e.g., Raukas & Teedumäe, 1997; Nõlvak et al., 2006; Meidla et al., 2014, Fig. 1C).

Material

The type locality of *P. wrangeli* was provided by Schmidt (1874) as a quarry belonging to Küti (German "Kurküll"), a manor near Viru-Jaagupi in northeastern Estonia. According to (Schmidt, 1858) the quarry was located south-west of manor house near Aruküla village (German "Arroküll"). The quarry was abandoned a long time ago and today is untraceable, its former location is indicated by the place name Lubjaahju (Estonian for Lime Kiln) (59°11'43.2"N 26°30'00.4"E) It exposed a pale-grey limestone of the Nabala and Vormsi stages (Rõõmusoks, 1966). The quarry was repeatedly visited by Schmidt (1858, 1874) because of its fossil richness. The abundance of conulariids was specifically mentioned and listed by Schmidt (1858, 1874) and is also documented in the SARV by an impressive number of more than 60 conularid specimens from the old Küti quarry. According to Rõõmusoks (1966) the richness is mainly limited to the Vormsi Stage; he listed brachiopods (mainly *Sampo hiiuensis* (Öpik), *Ilmarinia sinuata* (Pahlen), *Kiaeromena* (*Bekkeromena*) *vormsina* Rõõmusoks), hyoliths, gastropods, heliolitid tabulates, rugose corals, receptaculitids, and trilobites (mainly *Toxochasmops vormsiensis* Rõõmusoks). Two specimens of *P. wrangeli* from Küti are available from the collections of the NRM (NRM-Mo 153045, 153046). The lithological information available from matrix of these specimens is consistent with an origin from the Kõrgessaare Formation, Vormsi Stage. The Kõrgessaare Formation consists of an argillaceous, heavily bioturbated, greenish to yellowish pale-coloured mud-wackestone (Oraspõld and Kala, 1980).

Two specimens (Department of Geology at Tallinn University of Technology, GIT 812-34, GIT 612-35) were collected at the Sutlema quarry, west of Sutlema village, Rapla County, central Estonia (59°10'26.28"N, 24°37'2.62"E). The active quarry exposes the Saunja Formation (Nabala Stage) and the Kõrgessaare Formation (Vormsi Stage). Both specimens came from the Saunja Formation. At Sutlema the Saunja Formation contains a rich fauna and flora, dominated by green algae (*Vermiporella* Stolley, *Coelosphaeridium* Roemer, and an unidentified delicate dendroid form), gastropods (large *Murchisonia*-like forms, *Hormotoma insignis* Eichwald) and sponges. Additionally, bivalves, brachiopods [*Kiaeromena* (*Bekkeromena*) *ilmari* Rõõmusoks], cephalopods, conulariids, receptaculitids, rugose corals, trilobites, stromatoporoids, and dendritic graptolites (*Dictyonema* sp.) occur. The rich fauna of the quarry needs a detailed taxonomic examination. The Saunja Formation is more than 10 m thick at Sutlema and consists of a bioturbated, massively bedded, light-colored mud-wackestone, typical for the Baltic Limestone Facies (Kröger et al., 2019).

Three additional specimens come from drillcores, with little information on co-occurring fauna:

Specimen GIT 655-1 was collected from Kükita 24 drillcore (58°48'18.9"N 26°56'32.5"E), c. 4 km south of Mustvee, Mustvee Parish, west of Lake Peipsi, north-east Estonia, from depth 84.35 m, Tudulinna Formation, Vormsi Stage. The faunal content of the Vormsi interval of the drillcore is remarkably rich and comprises a delicate dendroid bryozoa (*Stictopora* sp.), a trilobite (*Isotelus* sp.), a hyolithid (*Dorsolinevitus vomer* Holm), a conulariid, and the putative cnidarian *Sphenothallus* (Vinn and Kirsimäe, 2014).

Specimen GIT 655-2 was collected from Ellavere drillcore (59° 0'52.42"N, 26° 1'24.89"E), c. 8 km south-east-east from Järva-Jaani, Järva County, north-east Estonia, depth 92.70 m, from the Nabala Stage. At the same horizon occurs a bellerophontid [*Megalomphala crassa* (Koken)], and a brachiopod [*Cyrtonotella kuckersiana* cf. *kuckersiana* (Wysogorski)]. The specimen GIT 655-2 occurs in a greenish - grey, bioturbated argillaceous skeletal of uncertain stratigraphy.

Specimen GIT 655-3 was collected from Mustvee 2322 drillcore, 3 km west of Mustvee, a village at the shore of the Lake Peipsi, north-east Estonia (58°50'5.41"N, 26°53'19.79"E), depth 69.15 m, from an interval within the Pirgu Stage. It occurs in a greenish gray, bioturbated, nodular argillaceous limestone of the Adila Formation.

Two specimens have been detected in the collections after completion of the analyses for this review: Specimen GIT 575-43, from Mäemetsa Quarry, Harju County, Saunja Formation, Nabala Stage; and specimen GIT 655-4, from Pala 70 drillcore at 143.90 m, Jõgeva County, Pirgu Stage.

Results

Morphology

The available specimens show some generalities in skeletal morphology. All specimens consist of four equidistant marginal pillars with diameters of up to 3 mm. The distance of the pillars increases at a constant angle of c. 13° toward a maximum preserved periderm diameter of c. 10–11 mm (Specimen GIT 612-34, Fig. 2). The four pillars are apically interconnected by irregularly spaced transverse diaphragms, which are slightly irregularly curved toward the apex of the pillars (Fig. 3). The pillars have a roughly semicircular cross section, which results from a relatively loose and irregular cone-in-cone succession of superimposed tubular shell layers exclusively on the inner side of the pillars (Fig. 3B–C, Fig. 4C, Videos S1–S2). The centers of the outer surface of the pillars are not covered with a continuous shell layer but expose, as a quasi-cross section, the complete succession of layers (Figs 3C–D). This results in a longitudinally carinate appearance of the outer surface of the pillars.

The diaphragms are continuations of individual pillar layers or sheets, with the oldest and apicalmost diaphragms representing the most distal, oldest pillar layers. The thickness of the diaphragms is similar to that of the laminae of the pillars, c. 10–80 μm. The shape of the diaphragms can be deeply conically curved, such as in specimen Mo 153045 (Fig. 4), or shallow bowl-shaped, such as in specimen GIT 655-3 (Fig. 5).

The transverse shape of the septa is nearly quadratically and the pillars are positioned at or near the four centers of the square margins, which would correspond to the midlines of the four periderm-faces of a conulariid (Fig. 4C, D).

The height of the individual cones of the pillars is more than what is preserved in the available specimens and thus exceeds 15 mm. Hence, the skeletal material accreted in form of clearly distinguishable, separate layers or sheets from the outer margins of the conch toward its center.

The apical end of the skeleton is open, and the pillars are not in contact with each other at their apical tip. The first septum occurs at a face width of 6 mm in specimen GIT 612-34 and at a face width of 8.5 mm in specimen Mo 153045.

In specimen GIT 655-3 the pillars are additionally thickened by massive flange-like skeletal sheets, which merge toward the periderm center with thick diaphragms (Fig. 5). A similarly thickened pillar section is preserved in specimen Mo 153045 (Figs 4A, B).

Notably in specimen Mo 153045, GIT 655-1, and GIT 655-3 skeletal fragments of thin cone shaped skeletal sheets or walls with a fragile lattice-like texture are preserved in close proximity of *P. wrangeli* (Figs 6A–C). These sheets in specimen Mo 153045 are longitudinally bent or folded forming sharp angles and flat faces. The shape of the sheets and the lattice-like structure is similar to co-occurring conulariid periderms (Fig. 6C, Video S3). In specimen GIT 655-1, fragments of a finely transversely annulated or ribbed sheet are preserved near the outer margin of a pillar (Figs 7A, D).

Microstructure

ESEM observations of *P. wrangeli* reveal that different parts of the skeleton have a similar microstructure, consisting of several distinct thin, phosphatic (fluoroapatite as evidenced from EDS, see Article S4) lamellae (Figs 7). This is similar as in conulariids and *Sphenothallus* (Brood, 1995; Vinn & Kirsimäe, 2015; Ford et al., 2016). The thickness of particular lamellae varies, ranging from c. 10 to 80 μm. As in *Sphenothallus*, the boundaries between particular lamellae may be more or less sharp. In several places, within a single lamella much thinner (c. 0.5 to 0.8 μm thick) laminae occur which may mark here a primary lamination. The microstructure of particular lamellae seems to be homogeneous, composed of tiny phosphate crystals. Sometimes, however, within particular solid lamellae, empty spaces may occur (Figs 7G–I). Such spaces have a limited extent and are filled by microcrystalline calcium phosphate. In some areas the interspaces between successive laminae contain phosphatic aggregations of thin (c. 1.5–1.8 μm in diameter), branching and diverging filaments. Some of the laminae also possess pores and empty chimney-like structures, with an inner diameter up to 4 μm (Fig. 7H). In the distalmost part of the skeleton of the specimen GIT 655-2 an extremely thin (up to 1 μm) outermost layer occurs, on which tiny (c. 16 μm in diameter), circular bumps (papillae) occur (Figs 7B, E, F). These structures may be isolated or associated in small groups. In some places, additionally smaller wrinkle-like structures (shrinkage features?) also occur (Fig. 7F). The wrinkled and papillate layer is covered from the inside by homogeneous skeletal layers devoid of such structures.

Discussion

Interpretation of the shell microstructure

The distinct lamellae of the skeleton of *P. wrangeli* partly contain fine irregular vertical perforations, chimney-like structures (Fig. 7H), and additionally in some places the lamellae-interspaces are filled with a layer of fine filamentous phosphatic aggregations (Fig. 7H–I). The chimney-like structures may be interpreted as original pore-like anatomical structures, because these structures appear to be limited to the papillate layer and there the shell lamina are often deflected toward the perforations. If so, it can be hypothesized that the papillate thin layer in specimen GIT 655-2 represents the remnants of the inner side of an external covering 'periderm'. However, the filled perforations in other areas of the shell are less regular, and the presence of filamentous micro-apatitic aggregations (Fig. 7I, Article S4) in some of the lamellae-interlayers can be best interpreted as a product of microbial and fungal degradation of originally organic-rich laminae. Hence these structures may indicate the presence of originally organic layers in between the phosphatic lamellae, which were post-mortem infested by boring microbial-fungal consortia. Similar, alternating phosphatic-organic layers also occur in skeletons of conulariids (Ford et al. 2016) and *Sphenothallus* (Vinn & Kirsimäe, 2015; Vinn and Mironenko, 2020).

Systematic affinities

The name giving enigma of *P. wrangeli* has two aspects: the first refers to the anatomical interpretation of the skeletal structures, and the second one, which relates to the first one, refers to its systematic affinity. Both mysteries can be partly solved with the new evidence from the examinations performed herein.

The preserved skeletal parts of *P. wrangeli* are invariably composed of calcium phosphate (presumably of apatite, such as in conulariids and *Sphenothallus*, Vinn & Kirsimäe, 2015). The 3D-reconstruction and ESEM examination of several well-preserved specimens reveals a consistent tetraradiate symmetry of the *P. wrangeli* skeleton with four semicircular marginal pillars, which are connected by irregularly spaced transverse diaphragms and which form a cone-like skeleton with an angle of c. 13°. The pillars and diaphragms are formed by a cone-in-cone structure of distinct sheets, which are accreted from the outer margin of the entire structure toward the center and from the apex toward the opening of the cone. Marginally, the diaphragms are not connected to each other except at the position of the pillars and thus do not form a closed structure. Similarly, the pillar-layers are open toward its margin and end abruptly at the outer surface of the pillars, resulting in a semicircular pillar cross-section and in a peculiar longitudinally lirate relief of the external pillar surface. The abrupt ending of the skeletal sheets at the margins of the diaphragms and at the external surfaces of the pillars suggests the presence of an organic outer cover or periderm, which is not fossilized, and which served as an attachment structure and matrix for the formation of diaphragms and the external pillar surface.

In summary, the skeleton of *P. wrangeli* shares a number of crucial characters, known in its combination only in the Conulariina: 1) the skeleton composed of calcium phosphate, 2) tetraradial, slender cone with thickened longitudinal septa at midline position and transverse diaphragms, 3) skeletal sheets forming irregularly and loosely spaced cone-in-cone structures. The poorly preserved, lightly mineralized phosphatic, transversely ornamented walls could be interpreted remains of a periderm. Therefore, *P. wrangeli* can be best interpreted as a conulariid with poorly mineralized marginal conch walls (periderm), phosphatic apical pillars and diaphragms. The pillars with their flat external surfaces can be best interpreted as homologue to the mineralized longitudinal septa at midline position in the Conulariina (see e.g., Ford et al., 2016; de Morales Leme et al., 2008).

Taking the general similarities and distinct constructional differences into account, it is evident that *P. wrangeli* should be placed to a separate conulariid family. Here we suggest the new family Palaenigmaidae fam. nov. for Conulariina with steeply pyramidal skeletons with a thin chitinophosphatic periderm that consist of four equidistant marginal pillars, without or with poorly biomineralized outer shell; the apical end of the skeleton is open, and the pillars are not in contact with each other at their apical tip. *P. wrangeli* is the only species of the Palaenigmaidae fam. nov.

Palaeoecology

In his original description, Friedrich Schmidt noticed the extraordinary abundance of co-occurring conulariids with specimens of *P. wrangeli* in the type locality of Küti, north-east Estonia (Schmidt, 1874). A co-occurrence of *P. wrangeli* with conulariids was described from Baltic Limestone boulders from Sweden (Holm, 1893). And conulariids are also relatively common in the Sutlema quarry, where two specimens of *P. wrangeli* have been found, as well (see above).

The compilation of conulariids in the SARV database allows for an investigation of the question whether this co-occurrence of *P. wrangeli* with conulariids represents a general pattern. Conulariids inhabited the eastern part of Baltica basin from the Darriwilian (Kunda Stage) onwards throughout the Silurian. They reached their Ordovician abundance climax within the Haljala Stage with 127 specimens in the collections from 18 different localities. A second abundance peak was reached during the Vormsi Stage, from which 51 specimens from seven different localities are known (Fig. 8). Most of the known specimens of *P. wrangeli*, including the type specimens, are also from the Vormsi Stage. This seems to support the idea that conulariids and *P. wrangeli* shared general habitat preferences and /or preservation pattern. Based on the specimens available for this study, *P. wrangeli* and the Late Ordovician conulariids of the eastern Baltica basin occur preferentially in depositional settings within an originally extraordinarily faunal-rich, calcareous soft substrate habitat.

Neither the extreme apices of *P. wrangeli*, nor that of co-occurring conulariids are known. Firmly skeletonized apical holdfast structures occur in Late Ordovician conulariids (Kozlowski, 1968; Brood, 995). These holdfasts are discoidal or rootlet-like, indicating differentiated conulariid attachment on hard substrate (discoids) and soft substrate (rootlets). Rootlet-like skeletal appendages are often interpreted as functioning for stabilization and attachment within soft substrate (e.g., Kozlowski, 1968; Seilacher & Macclintock, 2005). Additionally, elongated, stick-like conch forms often occur in mud-sticking bivalves, such as *Pinna* Linnaeus, which shares even more similarities with conulariids in having a subquadratic conch cross section (see e.g., Seilacher, 1984). A mud-sticking original life habit of *P. wrangeli* is therefore highly probable.

Conclusions

Paleaenigma wrangeli (Schmidt, 1874) is a rare fossil known from few specimens collected from Upper Ordovician limestone outcrops across northern and central Estonia and from erratic boulders in Finland and east central Sweden. The systematic affinities of the monotypic *Paleaenigma* were disputed. A thorough analysis of well-preserved specimens with X-ray computed tomography, scanning electron microscopy, and energy dispersive X-ray spectroscopy reveal that the skeleton of *P. wrangeli* is composed of distinct calcium phosphate (apatite) lamellae. The lamellae are partly porous and ornamented with distinct papillae and contain poorly mineralized interlayers. The skeleton consists of four pillars, which are connected by irregularly spaced diaphragms and which are marginally open. The diaphragms are quadratic in transverse view and the pillars are situated at the four sides of the diaphragm squares. In few specimens remains of thin, poorly preserved transversally ornamented apatitic tube-forming walls are preserved near the distal margins of the pillars. Therefore, *P. wrangeli* can be best interpreted as a conulariid with poorly mineralized marginal conch walls (periderm), phosphatic apical pillars at midline position, and diaphragms. The new monospecific family Palaenigmaidae fam. nov. is proposed for *P. wrangeli*. Conulariids often co-occur with *P. wrangeli*. A comparison of other conulariid occurrences in Estonia with *P. wrangeli* occurrences indicates that these fossils are most abundant in depositional settings within an originally extraordinarily faunal-rich, calcareous soft substrate habitat. Based on its general morphology *P. wrangeli* can be interpreted as a poorly mineralized conulariid with a mud-sticking original life habit.

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Figure 1

Occurrences of *Palaenigma wrangeli* (Schmidt, 1874) in north Estonia

(A) Map of Baltoscandia with national boundaries and capitals (black dots). (B) Map of Estonia with *P. wrangeli* occurrences discussed herein (yellow dots), and with outline of Late Ordovician facies belts (from Harris et al., 2004). (C) Middle – Late Ordovician Regional stages of Baltoscandia (stars mark occurrences of *P. wrangeli*. Hirn., Hirnantian. Map data: R Package „maps" Version 3.3.0 (https://cran.r-project.org/web/packages/maps/maps.pdf).

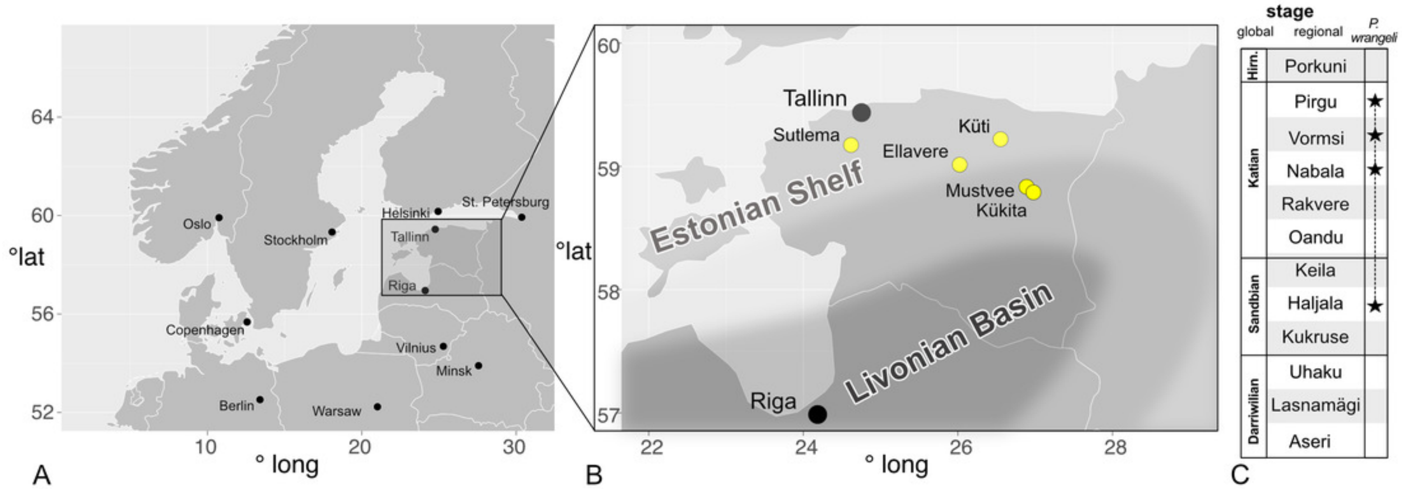


Figure 2

X-ray computed tomography image of *Palaenigma wrangeli* (Schmidt, 1874), specimen GIT 612-34, from Sutlema quarry, west of Sutlema village, Rapla County, Estonia, Nabala Stage.

(A) Lateral view. B. Lateral view 90° rotated along the growth axis relative to A. (C) Lateral view parallel to two pillars. Scale applies to all figures.

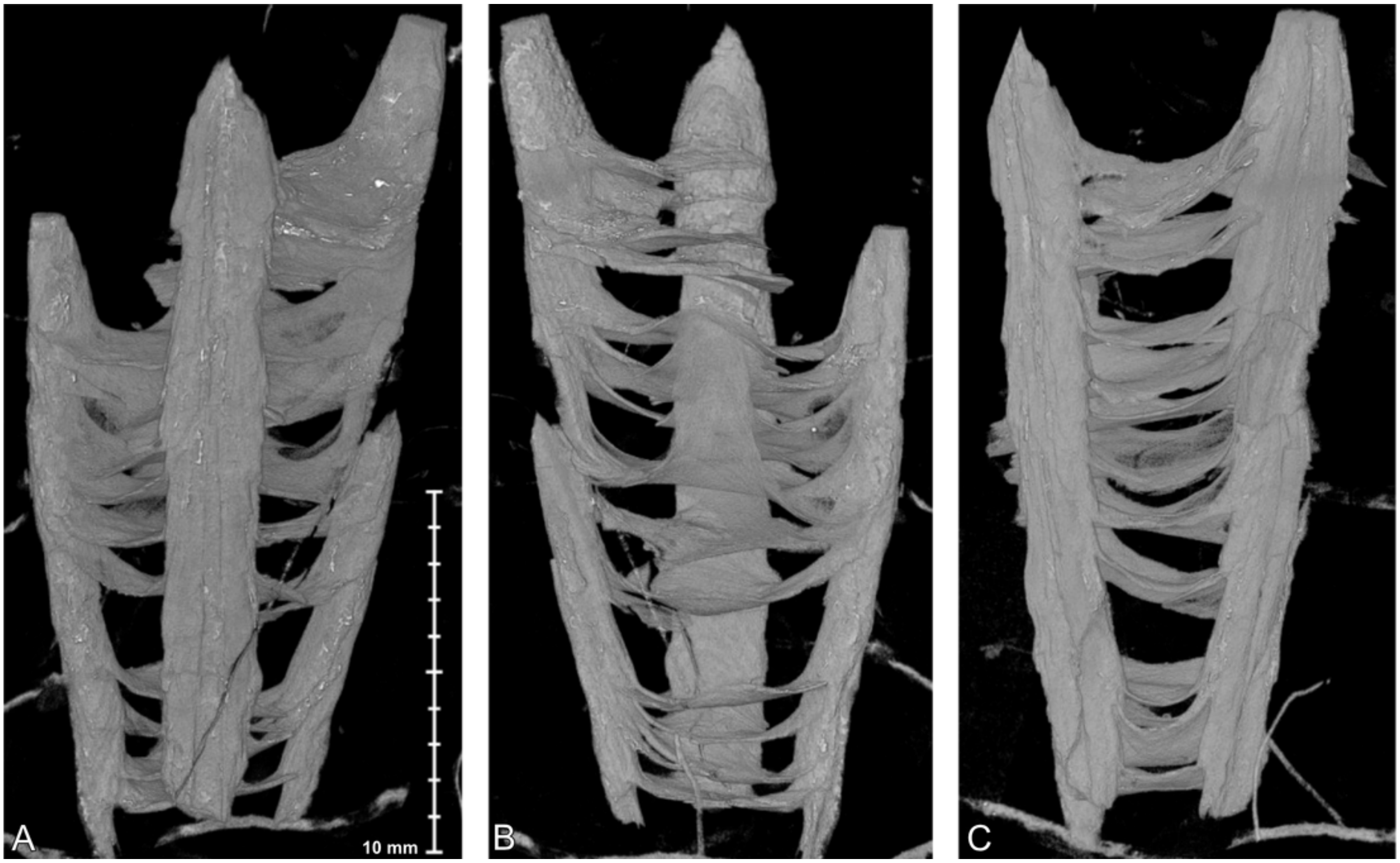


Figure 3

X-ray computed tomography cut of *Palaenigma wrangeli* (Schmidt, 1874)

(A), (B) Specimen GIT 612-34, from Sutlema quarry, west of Sutlema village, Rapla County, Estonia, Nabala Stage. A. Sagittal cut. B. Transverse cut. (C), (D) Specimen NRM-Mo 153045, from Küti quarry, near Viru-Jaagupi in northeastern Estonia, Vormsi Stage. C. Transverse cut. D. Sagittal cut. Note the irregular spacing of the diaphragms and the continuation of the diaphragm – pillar layers in A and D, and the open half-circle cross section shape of the pillars in C and D. Scale applies to all figures.


A
5 mm
B
C
D

Figure 4

X-ray computed tomography image of *Palaenigma wrangeli* (Schmidt, 1874), specimen NRM-Mo 153045, from Küti quarry, near Viru-Jaagupi in northeastern Estonia, Vormsi Stage

(A) Lateral view, scale applies to A, (B) Lateral view 180° rotated along the growth axis relative to A. C. Adapical view, scale applies to C, D. (D) Adoral view.

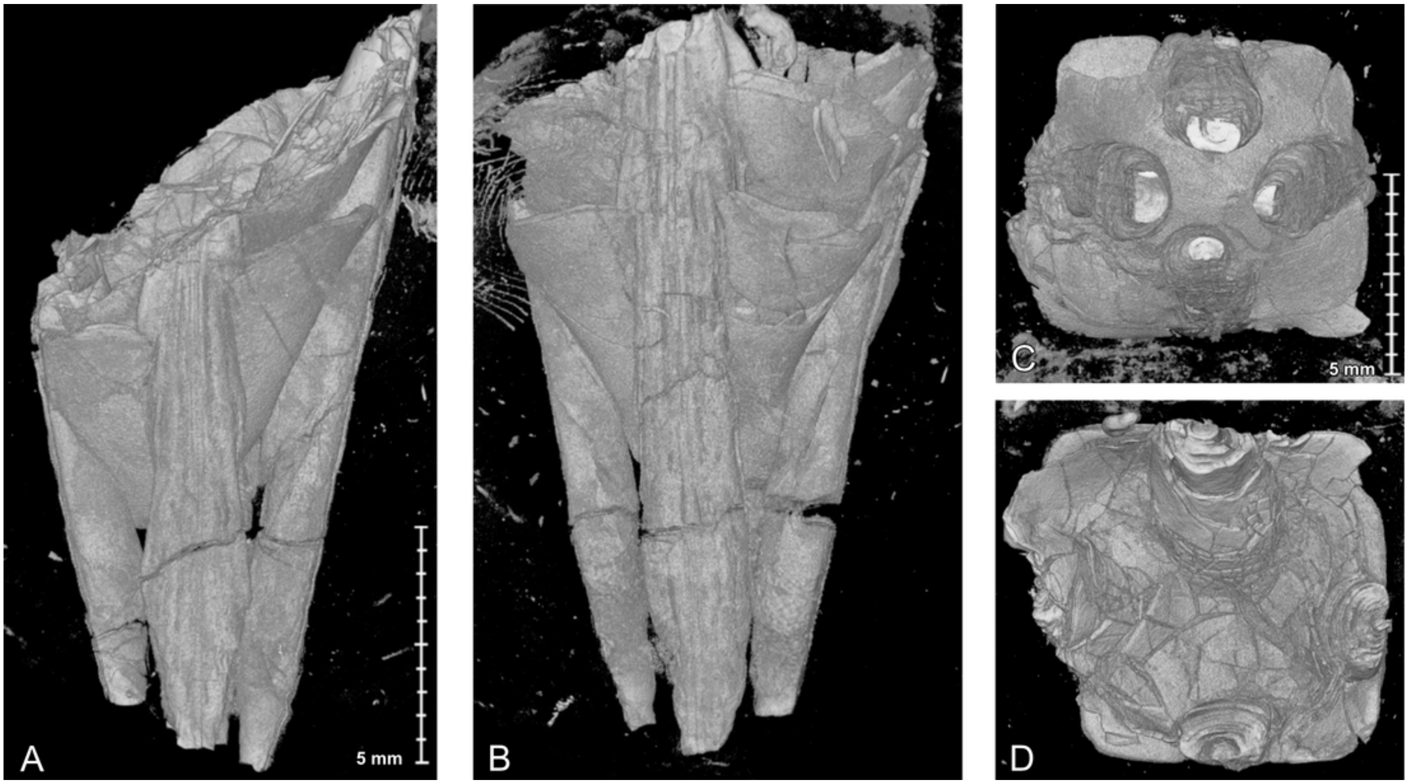


Figure 5

X-ray computed tomography image of *Palaenigma wrangeli* (Schmidt, 1874), specimen GIT 655-3, from Mustvee 2322 drillcore, west of Mustvee, north-east Estonia, Pirgu Stage

(A) Lateral view. (B) Lateral view 90° rotated along the growth axis relative to A. (C) Lateral view 180° rotated along the growth axis relative to A. Scale applies to all figures.

Figure 6

X-ray computed tomography image of *Palaenigma wrangeli* (Schmidt, 1874) and conularid fragments

(A) Lateral view of specimen GIT 655-3 with unidentified skeletal debris in surrounding sediment matrix and fragment of conulariid (upper right). (B) Lateral view of specimen NRM-Mo 153045 with unidentified skeletal debris in surrounding sediment matrix and fragment of conulariid (upper right). (C) Lateral view of conulariid GIT 812-35-1, from Sutlema quarry, Nabala stage, note also the disc-like shadow of a crinoid ossicle in the sediment matrix.

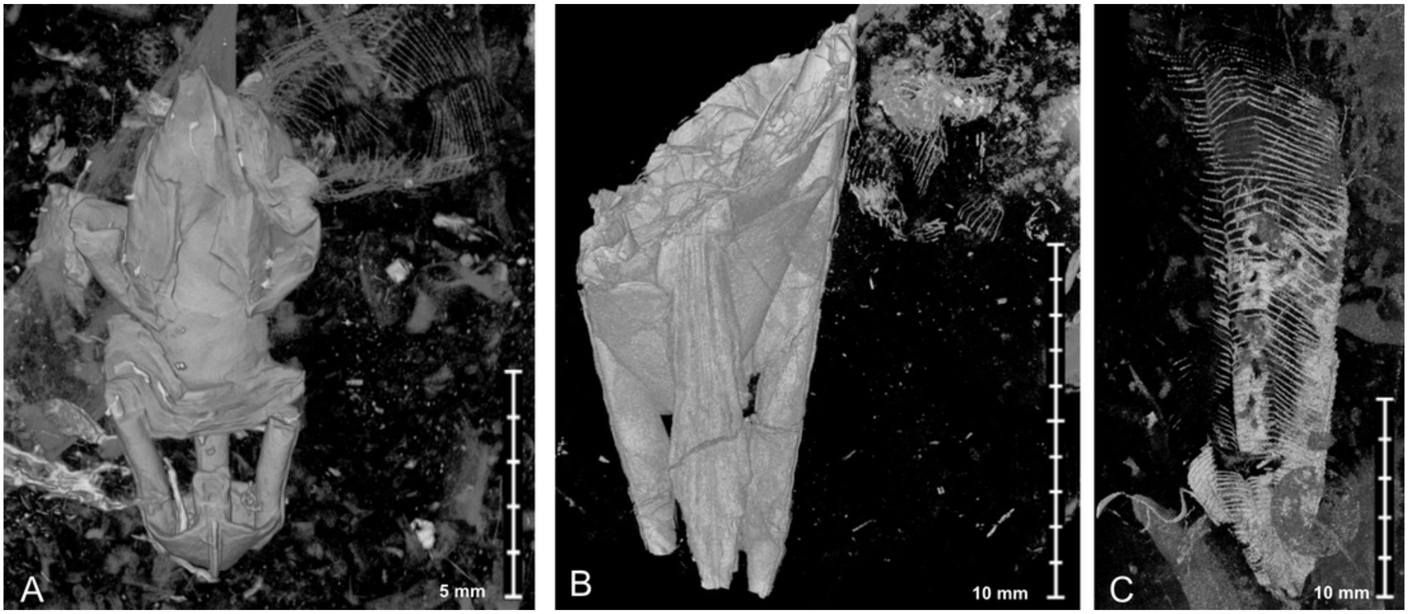


Figure 7

Scanning electron images of *Palaenigma wrangeli* (Schmidt, 1874)

(A), (D) Specimen GIT 655-1, from Kükita 24 drillcore, Mustvee Parish, north-east Estonia, Vormsi Stage, showing fragment of a transversally ornamented periderm? near external surface of a pillar. (B–C), (E–I) Specimen GIT 655-2, from Ellavere drillcore, Järva County, north-east Estonia, Nabala Stage. B, E, F. Area with distinctive papillate surface and with wrinkles (arrow in F). G–I. Details showing lamellate conch cross section with empty or filamentous interspaces (arrow in G). Note also the chimney like structures (arrow in H).

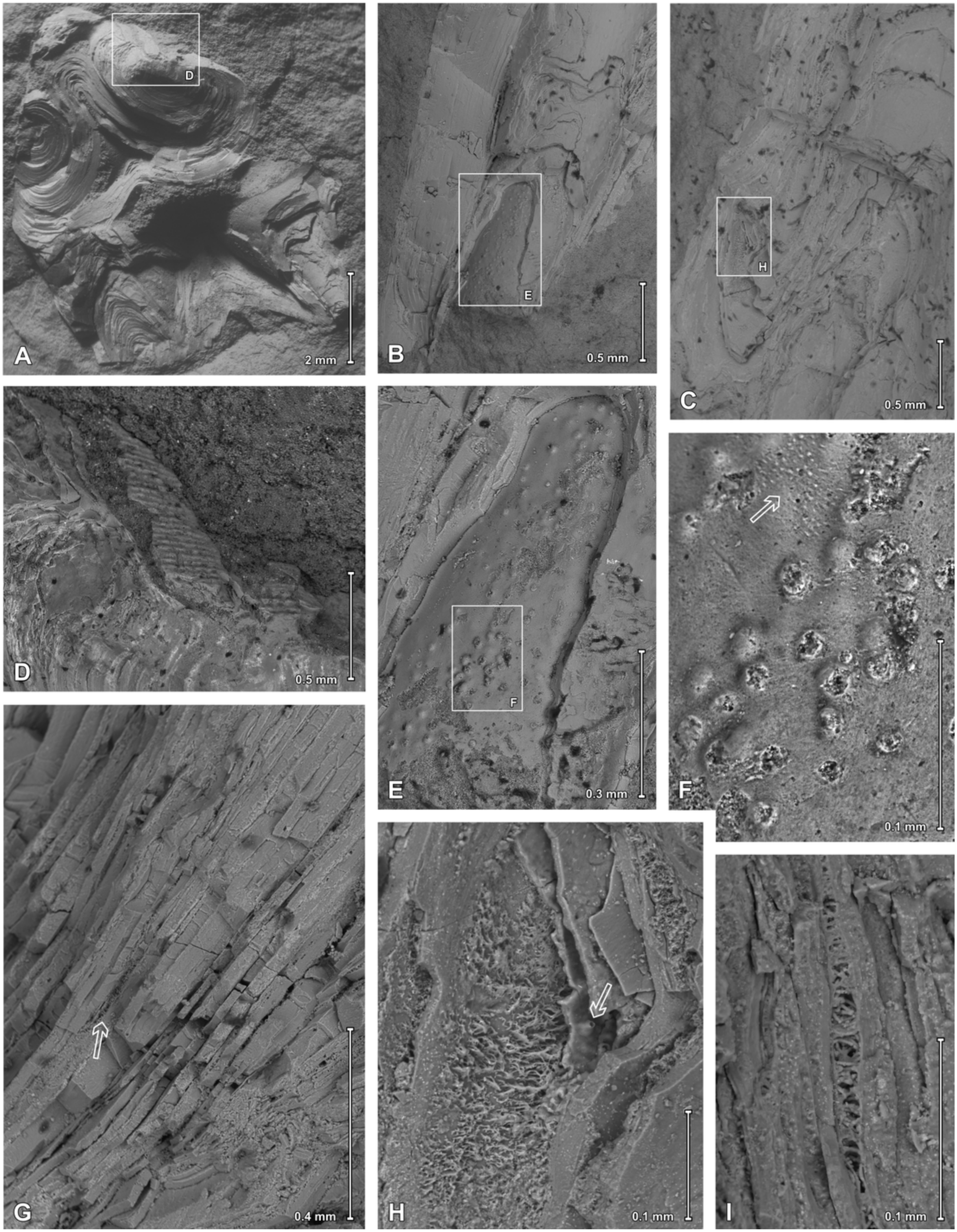
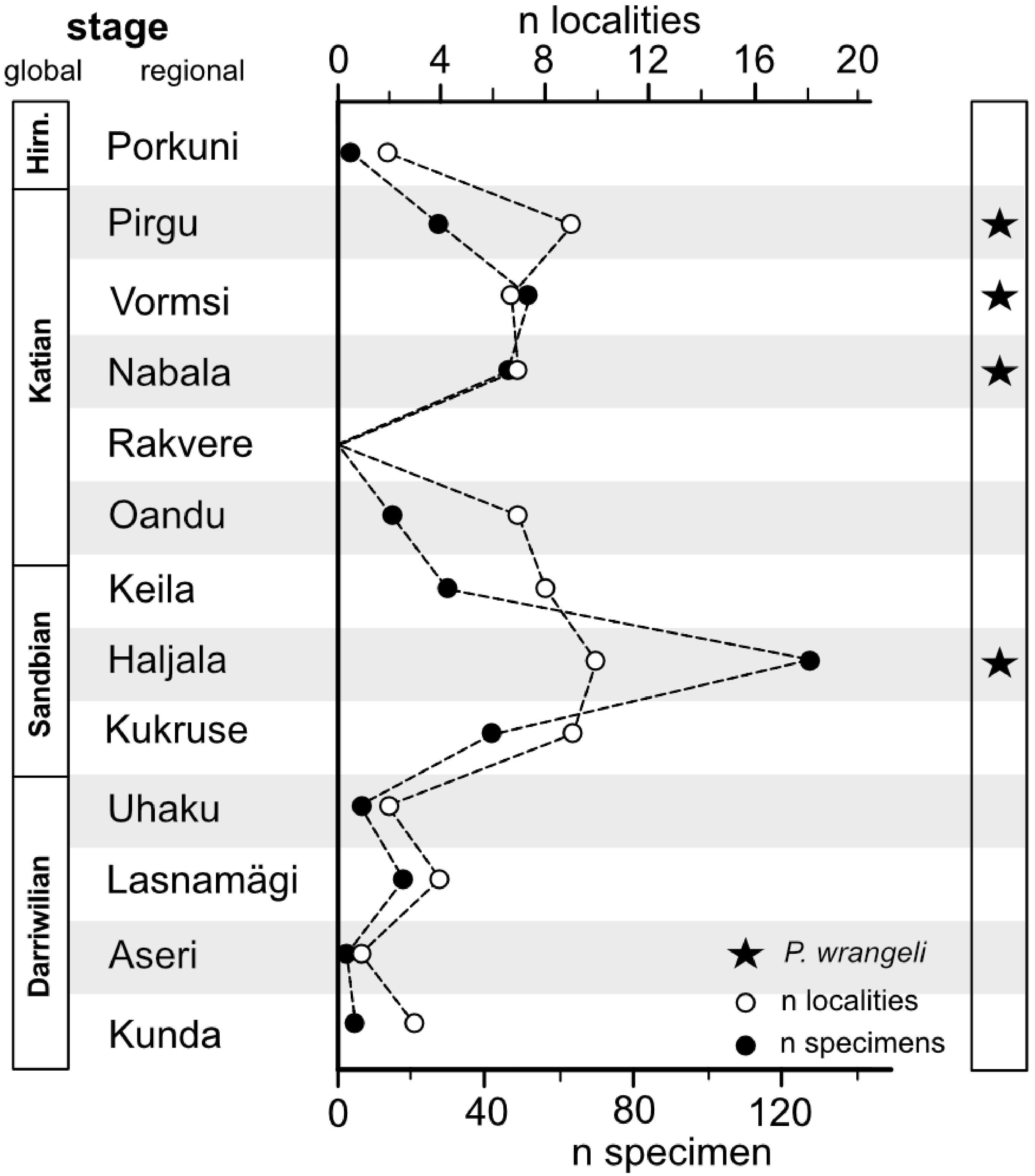

A
D
2 mm
B
E
0.5 mm
C
H
0.5 mm
D
0.5 mm
E
F
0.3 mm
F
0.1 mm
G
0.4 mm
H
0.1 mm
I
0.1 mm

Figure 8

Abundance (= frequency of occurrences) of conulariids in Estonian Ordovician strata and stratigraphic occurrence of *Palaenigma wrangeli* (Schmidt, 1874)

Hirn., Hirnantian; n, number. Data: downloaded from SARV at 08.04.2021(see also Methods section and Data S5)


stage
global
regional
n localities
0
4
8
12
16
20
Hirn.
Katian
Sandbian
Darriwilian
Porkuni
Pirgu
Vormsi
Nabala
Rakvere
Oandu
Keila
Haljala
Kukruse
Uhaku
Lasnamägi
Aseri
Kunda
★ P. wrangeli
○ n localities
● n specimens
0
40
80
120
n specimen