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**Article**

# Problematic scale-like fossils from the Ordovician of Siberia with possible affinities to vertebrates

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With 4 figures

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**Abstract:** Microtomography and sectioning of the morphologically variable scales of *Kodinskaspis angarensis* gen. et sp. nov. from the Mamyry Formation of the Irkutsk Basin of Siberia (early Mid Ordovician, 460 Ma) show that their formation started from minute conical thin-walled units (cusps). The whole body of the cusp, as well as the structurally identical phosphatic lamellar tissue common for the whole scale, was secreted basally. V-shaped series of cusps accreted to the anterior margin of the scale during its growth. The mineral tissue of the Siberian scales resembles atubular dentine of some Late Ordovician to Early Silurian (450-440 Ma) fish scales from the same region of the world, associated with regular dentine or bone. A tissue similar in structure, secretion mode and location is known also in conodonts, referred to as the basal body tissue. Its homology with dentine finds some support from this new evidence. It is suggested that the new finding represents the geologically oldest and morphologically simplest member of the Siberian tesakoviaspidids.

**Key words:** Dentin, enamel, agnathans, conodonts, Ordovician, Siberia.

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## 1. Introduction

Unavoidably, interpretation of the early evolution of vertebrate skeleton and debates on its origin largely depend on knowledge of histology and developmental biology of present day organisms. The tissues occurring in teeth and scales of extant fish can be identified even in the most ancient fossils of vertebrates. The oldest histologically known probable pteraspidomorph *Sacabambaspis* from the late Llanvirn (Darriwilian; early Mid Ordovician, about 460 Ma) of Argentina had the plates of its armour composed of acellular bone with dentine and enameloid comprising the tubercles (Sansom et al. 2005). External morphology of armoured agnathans of approximately the same age from Australia is similar enough (Young 2009) to suggests the same internal structure. Even the tissue as derived as the cellular bone was reported in Ordovician armoured vertebrates (Karatajute-Talimaa & Novitskaya 1997; Sansom et al. 2012).

A kind of the mineral tissue (lamellin) significantly different from those represented among extant vertebrates was found in the mongolepidid scales from the Late Llandovery (Early Silurian, 435 Ma) of Mongolia (Karatajute-Talimaa 1998). This was a compact lamellar-calcospheritic tissue deposited basally (centripetally) and apparently representing atubular dentine (Karatajute-Talimaa & Smith 2004; Sire et al. 2009). In the probable chondrichthyan mongolepidids it was supplemented basally with more sophisticated kinds of dentine and its derivatives, but in *Tesakoviaspis* from the Early Llandovery (about 440 Ma) of the Irkutsk and Podkamennaya Tunguska basins of Siberia only a basal cup interpreted as acellular bone is developed (Karatajute-Talimaa & Predtechenskyj 1995; Karatajute-Talimaa & Smith 2004). These authors also reported occurrences of tesakoviaspid scales in the Late Ordovician strata of Podkamennya Tunguska River region. Both the mongolepidids and the tesakoviaspidids are known only from isolated scales, and their direct rela-

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tionship seems unlikely. Nevertheless, the evolutionary importance of lamellin may appear significant owing to discovery of even older scales from the same area of the Irkutsk Basin, composed exclusively of a tissue similar to lamellin, which is the subject of this work. It may be meaningful that the histology and inferred mode of secretion of these scales is virtually indistinguishable from that of the conodont basal body tissue.

## 2. Geological age of the material

Locality 791 in the "wide flowing Angara region" (Moskalenko 1984) was on the left bank of the Angara River about 5 km downstream of the former village Rozhkovo. The sample that yielded the fossils under study was collected by the junior author from the up to 0.5 m thick bed 19-2 of dark-grey organodetrital limestone that formed a lens-like discontinuous bed, disappearing laterally along the exposure. The fossils include abundant shell detritus, gastropod conchs, probable monoplacophorans, and fragmentary carapaces of the arthropod *Obrutchevia*. This bed belongs to the mostly argillaceous lower unit of the Badaranovo Formation, representing the lowest fossiliferous horizon within it. After a dam on the Angara River near Kudinsk was constructed, this part of the bank was overgrown by vegetation, no longer being cleared by spring floods. The senior author was unable to find any exposure of the rock in this area during an expedition in 2007.

In the Ordovician, the Siberian Platform was a separate continent with faunas biogeographically distinct from those of other regions of the world. Only some species of pelagic organisms had a wide enough distribution to enable age correlation (e.g., Dumoulin et al. 2002). In the Angara section, the conodonts may serve this purpose but their knowledge is at a preliminary stage, with the standard apparatus-based taxonomy applied to only a few species, none from the Badaranovo Formation. A brief overview of the evidence is thus necessary. Conodont assemblage (Moskalenko 1984) contains *Cardiodella lyrata*, *C. tumida*, *Coleodus mirabilis*, *Leptochirognathus longus*, "*Lonchodus*" sp. A, *Microcoleodus* (?) *triangularis*, *Neocoleodus dutchtownensis*, *Polyplacognathus angarense*, *Ptiloconous longidentatus*, *P.* (?) *costulatus*, *P.* (?) *proprius*, and *Trichonodella* cf. *barbara*. In biological (apparatus) taxonomy, these seem to represent a set of elements of a coleodontid and an early balognathid with elaborate platform element morphology. The name *Coleodus mirabilis* Moskalenko, 1970 is available for the former species (Moskalenko 1970), although additional research and comparison with the North American Midcontinent type species of the genus is necessary. The *Coleodus* apparatus is known to comprise three pairs of elements, two of them sparsely denticulate and one ribbon-like (Liu et al. 2006, 2007). The most distinctive balognathid "*Polyplacognathus*" *angarense* Moskalenko, 1984 (Moskalenko 1984) is unknown outside Siberia. Higher up in the section it co-occurs with *Phragmodus flexuosus* that indicates *Pygodus serra* Zone of the Llanvirn.

According to (Kanygin et al. 2010) the Mukteian stage of Siberia correlates in age with the upper part of the Baltic Kundan (earliest Llanvirn, early Darriwilian). The fossil assemblage suggests a shallow-water marine environment.

## 3. Methods

The specimens were recovered from limestone with the standard technique applied to conodonts, that is with diluted acetic acid. The material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

The specimens studied for microstructure under scanning electron microscope (SEM) were embedded in epoxy resin, ground and polished. They were etched with 0.5 % orthophosphoric acid until a relief visible in reflected light under microscope developed. The time of etching was about ten minutes. The blocks with embedded specimens were then attached to the stub and covered with platinum.

Two specimens were scanned in the X-ray microtomograph Xradia MicroXCT-200 with pixel size 1.01 µm.

## 4. Description

### 4.1. External morphology of scales

The available material is small but even the forty mostly fragmentary specimens in hand show a wide range of morphologies. These are triangular or rhomboidal plates with roof-like sides and well delimited boundaries (Fig. 1), which makes them different from pieces of phosphatised arthropod cuticles with similarly simple microstructure (Briggs & Fortey 1982), common in the Ordovician of Siberia. All scales have their external surface covered with minute smooth conical cusps. Their surface is glossy unlike the main body of the scale, which is matte. The cusp base may be swollen (Fig. 1g, h) or may be slightly constricted, exposing then increments of the tissue (Fig. 2c, d). In some speci-

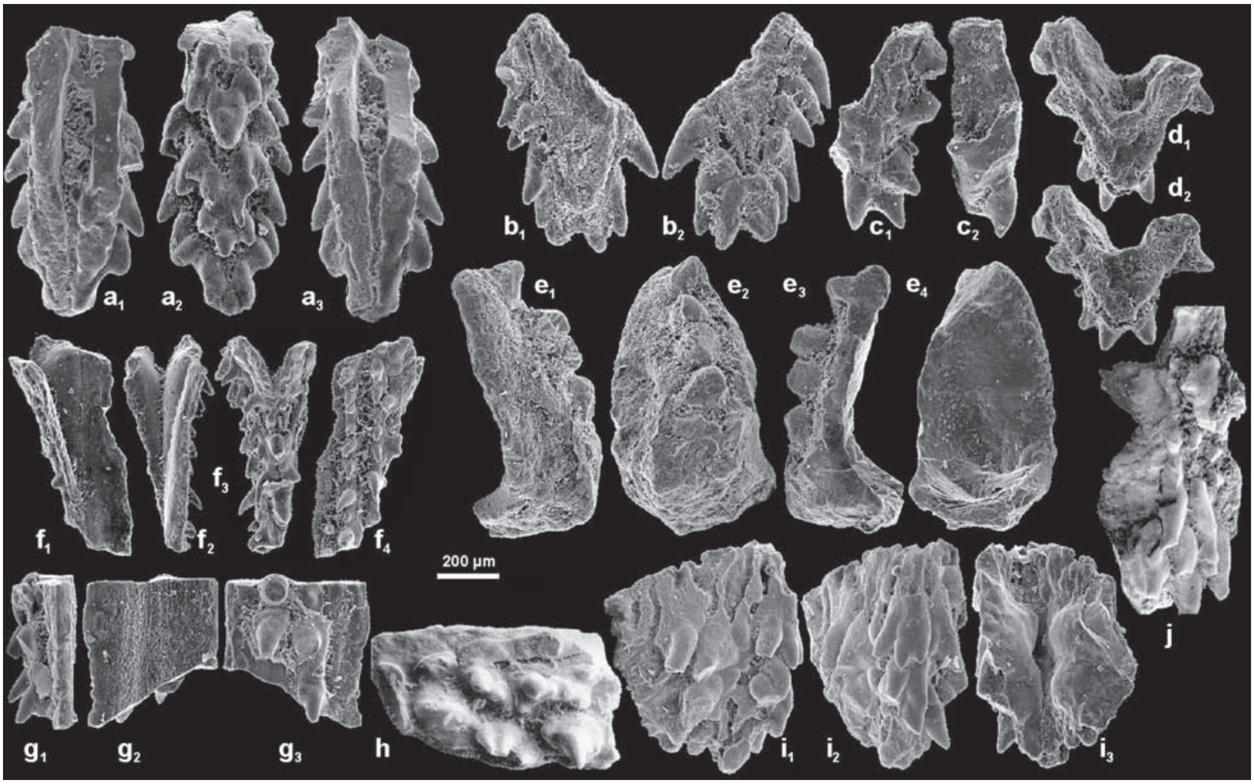

**Fig. 1.** Scanning electron microscope pictures of *Kodinskaspis angarensis* gen. et sp. nov. scales. **a** – ZPAL c.XXII/49 with symmetrical appearance and narrow basal cavity, note three levels with feather-like disposition of cusps; the upper end is interpreted as anterior. **b-d** – ZPAL c.XXII/44, 55 and 47 with wider disposition of cusps and weak mineralization of their bases. **e** – ZPAL c.XXII/51 with conical appearance and vertical disposition of cusps. **f** – ZPAL c.XXII/48 with thin wall and strong asymmetry, note four levels with linearly distributed cusps. **g** – ZPAL c.XXII/46 with flat base and linear distribution of cusps. **h** – ZPAL c.XXII/56 with flat base and irregular distribution of low, vertically oriented cusps. **i** – ZPAL c.XXII/50 with narrowed apex and widely gaping base, note exposed pulp cavities of some cusps. **j** – ZPAL c.XXII/47, incomplete large irregular plate.

mens cusps near the anterior margin of the scale have their pulp cavities exposed (Fig. 1i). The cusps are arranged in rows that are usually regular, of V-shaped appearance (Fig. 1a, f), but the rows may be hardly discernible in a chaotic pattern (Fig. 1h-j).

The V-shaped rows of cusps are parallel to each other. The more basal and posteriorly located rows have a wider extent. In some narrow scales the successive rows meet at a narrow angle and their course is parabolic (Fig. 1a). In wider scales the rows meet posteriorly at wider angle and the scale is less elevated (Fig. 1b-d).

Some scales are virtually symmetrical, others have one side much better developed and may be twisted along the axis (Fig. 1f).

Seen from the basal side, the surface of the pulp cavity is smooth and may be bulbous (spherulitic), especially in its centre (Fig. 1e). Spherulites vary in size. They are usually irregularly distributed but in one specimen (Fig. 1g) they are minute and arranged linearly in longitudinal rows. The pulp cavity of the whole scale is usually narrow posteriorly and gaping anteriorly (Fig. 1a). In some specimens it is wide, virtually conical (Fig. 1e); in others roof-like with a narrow furrow extending along the whole scale length (Fig. 1f). The furrow may be enclosed by basal increments, forming then an internal channel. Fragmentary specimens show virtually flat appearance, but it is unclear whether these are portions of strongly asymmetric V-shaped scales or irregular plates.

### 4.2. Histology

Sections of the scales show their lamellar internal structure. The laminae are regularly spaced but their

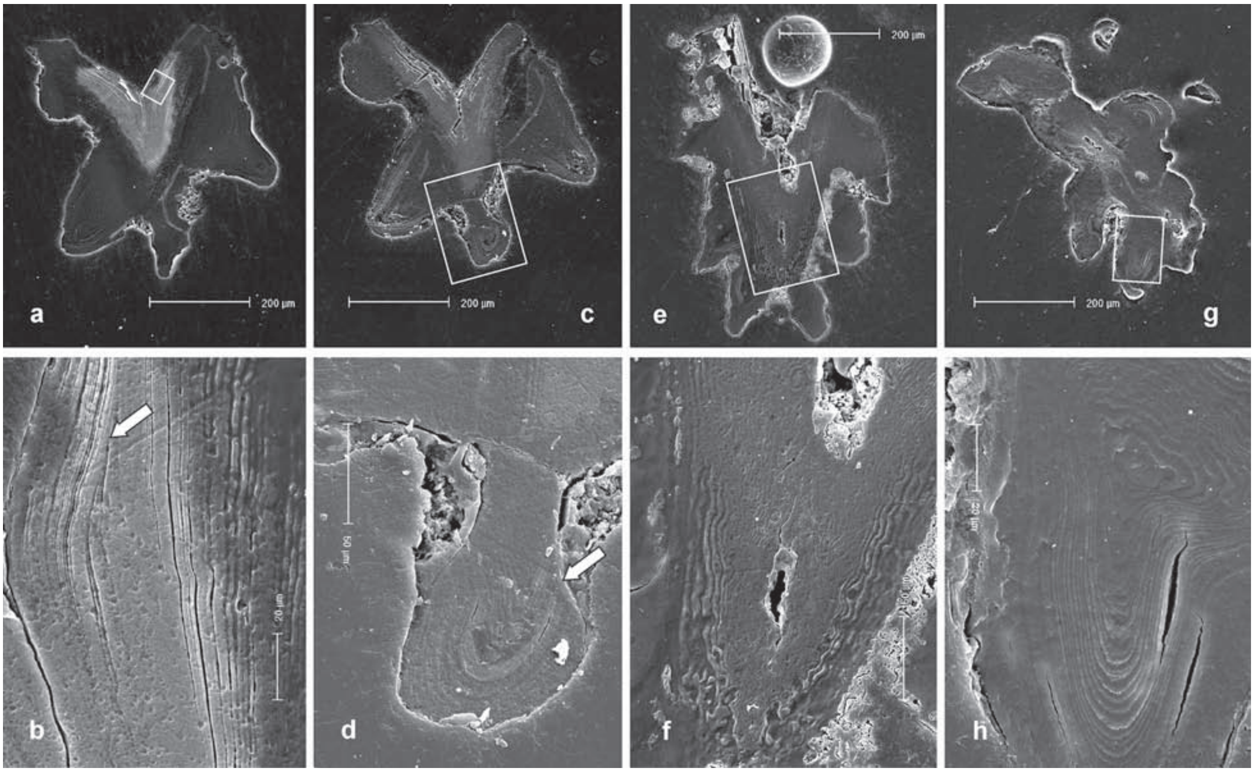

**Fig. 2.** Etched sections of *Kodinskaspis angarensis* gen. et sp. nov. scales under SEM. **a, b** – ZPAL c.XXII/52, general view and lamellar structure of the base (angular contact between lamellae arrowed). **c, d** – Same specimen after additional grinding and etching shows a cap-like cusp with its base narrowing during growth (lamellae reaching surface arrowed; note the rock matrix preserved around the neck). **e, f** – ZPAL c.XXII/45 with spherulitic growth of the tissue in later stages of filling the pulp cavity. **g, h** – ZPAL c.XXII/54 showing regular spacing of lamellae, presumably corresponding to daily increments.

thickness depends on location in respect to cusp tips and changed during growth. On cusp sides and in central parts of the base they are about 2 µm thick (Fig. 2h), near termination of the scale growth they diminished to less than 0.5 µm (Fig. 2b). In the apical parts of the scale pulp cavity, the laminae are not parallel to the cusp surface or the surface of the cavity, but form spherulites of up to 10 µm diameter (Fig. 2f). There is a clear linear boundary between conical cusps and the tissue forming the whole scale pulp cavity (Fig. 3b, c).

### 4.3. Mode of growth

Microtomographic longitudinal sections passing across the cusp tips (Fig. 3b-e) show that their secretion started as a cap-like thin-walled unit (Fig. 3d, e). The unit apparently corresponds to the glossy part of a cusp. The layers are strictly parallel to the cusp surface and continue from one to another cusp of the same V-shaped series but in some cusps with narrowed base (Fig. 2d) they are larger and larger basally, extending beyond the cusp basal margin. As indicated by differences in local thickness of laminae the growth rate was higher in the tips of the cusp pulp cavities and eventually they were filled over the whole lower surface of the scale. As shown by sections studied under SEM, it required about 50 laminae to fill the cusp completely. A uniform conical pulp cavity for the whole scale then developed with a clear demarcation of its initiation by a flat boundary surface, although locally the transition may be gradual (Fig. 3b, c). The secretion rate, inferred from laminae thickness, was the highest in the posterior part of the scale and spherulites may develop there. In result, this region of the pulp cavity is constricted and forms the narrow furrow, which may be enclosed basally in robust specimens, presumably most advanced in growth. This may mean that the size of scales was determined and their further growth resulted only in thickening of their base. In the anterior part, the scale inner surface

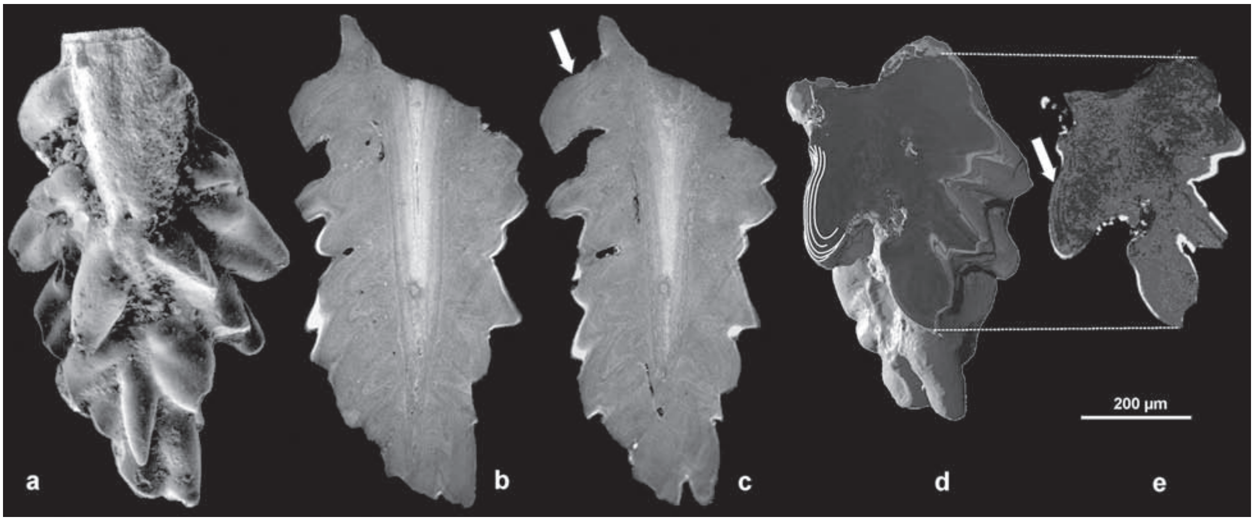

**Fig. 3.** Selected X-ray microtomographic sections of *Kodinskaspis angarensis* gen. et sp. nov. scale ZPAL c.XXII/53 (**b-e**) and its external view under SEM (**a**). Arrowed are parts of the sections where lamellae reach the surface indicating that growth started from separate caps and proceeded basally; inferred boundaries between lamellae on an axially sectioned cusp marked with white lines (**d**).

remains flat and the growth increments are strictly parallel. This stage took another circa 45 increments.

The glossy parts of the cusps may be interpreted as odontodes, this is isolated hard superficial structures of the skin consisting of a core of dentine, or dentine-like tissue (Ørvig 1977; Sire & Huysseune 2003; Fraser et al. 2010). If these were anatomical structures of vertebrates, they were separated from the layer of ameloblasts by a basal membrane. There is no evidence of any mineralised tissue at the surface that could be secreted by ameloblasts and correspond to enamel. The whole body of the cusp was secreted basally (Figs. 2b, 3e), presumably by an epithelium composed of odontoblasts.

New cusps were apparently added at the anterior margin of the scale during its growth, initially having open pulp cavities. The V-shaped units with usually straight rows of cusps emerged sequentially at the medial angulation of the scale near its anterior margin.

Dermal elements equivalent to odontodes develop relatively late in the ontogeny of present-day vertebrates. In teleosts, which are the closest relatives for which data are available, it occurs about 30 days after fertilisation (Sire & Huysseune 2003). The acellular mineral tissue of the Siberian scales resembles enamel in its microstructure (but not in the mode of secretion) more closely than its probable homolog dentine; also in thickness and regularity of probably daily rhythmic increments (Dzik 2008). If they truly correspond to days, it took circa 50 more days to unify odontodes into a mineralised flat scale and 45 more days to the complete formation of the scale. The growth was terminated, as shown by condensation of increments near the basal surface of the scale. This gives about half a year from fertilisation to maturity.

## 5. Discussion

### 5.1. Lamellin in early vertebrates

Simple odontodes built of lamellar tissue were identified in scales of the earliest Silurian *Tesakoviaspis concentrica* (Karatajute-Talimaa & Predtechenskyj 1995; Karatajute-Talimaa & Smith 2004) and the slightly geologically younger mongolepidids (Karatajute-Talimaa & Novitskaya 1997). The Late Ordovician and Early Silurian complex scales of *Tesakoviaspis* had cyclomorial growth, with sequentially added odontodes surrounding the central one. Each odontode grew centripetally around its separate pulp cavity. This growth pattern makes them different from the new early Mid Ordovician form, in which new cusps (proposed odontodes) are added in rows only along the anterior scale margin. Moreover, the acellular bony base was added in *Tesakoviaspis* scales below the odontodes. All layers of bone in *Tesakoviaspis* are penetrated with vertical probable tubuli from the basal surface (Karatajute-Talimaa & Predtechenskyj 1995; Karatajute-Talimaa & Smith 2004). We propose that the tissue forming the conical pulp cavity of the whole scale of the new Siberian form is homologous to the acellular bony base of *Tesakoviaspis*, despite the different histology.

*Tesakoviaspis* and the new probable vertebrate occurred in the same region, representing a separate biogeographic province (Kanygin et al. 2010), in successive rock units. It is likely that they represent a sequence of evolutionary transformation. The mongolepidids from younger strata of Mongolia, still in geographic proximity, show even more complex histology of the scales and are believed to represent chondrichthyans. This may mean that the histologically simple status of the new Siberian scales is plesiomorphic for the early vertebrates.

The Siberian early Mid Ordovician form is among the oldest known scale-bearing vertebrates, but possibly not the oldest. It predates the histologically best-known North American discoveries, including *Astraspis* (Sansom et al. 1997). The oldest discoveries of the *Sacabambaspis* in Argentina and Oman are probably of similar age (Sansom et al. 2005, 2009). The imprints named *Pircanchaspis* from the the Pircancha Formation of Bolivia, dated as early Arenig (about 475 Ma), has been identified as possible agnathans based only on fingerprint ornamentation (Erdtmann et al. 2000). Also the Stairway sandstone, with the Australian early agnathan *Arandaspis* is of age similar to the Siberian find (Davies et al. 2011). Scales of probable chondrichthyan *Areyongalepis* from the Stokes Siltstone (Young 1997) appear to be of early Caradoc (Sandbian, earliest Late Ordovician, 455 Ma) age (Zhang et al. 2003) but another probable chondrichthyan of Early Darriwilian age, *Tantalepis*, is known from Australia (Sansom et al. 2012). Its internal structure remains unknown but external aspects of the scales suggests that they are composed of three odontodes each, of size comparable to those in the Siberian scales. Relationships of the Late Cambrian to Mid Ordovician *Anatolepis* was hotly debated, identification of probable dentine being used as a support of vertebrate affinities (Smith & Sansom 1995; Smith et al. 1996; Turner et al. 2004). The external morphology of tubercles ornamenting plates of *Anatolepis* is different from other Ordovician agnathans and, if it was truly an armoured agnathan, it represents a separate lineage.

Both the unusually simple histology and ancient geological age means the Siberian agnathan remains are important in discussing the origins of the vertebrate mineralised skeleton. The lack of separate external layer of enamel-like tissue supports the idea that enameloid arose from dentin and enamel from enameloid more than once in vertebrate evolution (Kawasaki et al. 2005). The question of possible agnathan-conodont relationship may appear relevant in the context.

### 5.2. Comparison with conodonts

Skeletal remains of vertebrates are very rare in the Ordovician despite extensive sampling for conodonts over the whole world. Elements of conodont apparatuses are extracted from rocks using the same method as for fish teeth or scales (ichthyoliths), all being of identical mineralogy and similar structure. The early agnathans and gnathostomes apparently preferred more inshore shallow-water environments than the generally open-sea conodonts, but different ecology does not preclude evolutionary relationship and homology of structures.

Conodonts (euconodonts) are the only animals other than vertebrates with their phosphatic skeleton secreted at the same time from above, by the epithelial cover of ameloblasts (like enamel or ganoine), and basally by cells of presumably mesodermal (or ectomesodermal origin), thus homologues (or at least analogues) of odontoblasts (like dentine and dentine-derived tissues). The idea of homology between the conodont oral apparatus elements crown tissue and enamel, and the basal body (basal filing) tissue with dentine was forwarded by Schmidt & Müller (1964). It has been supported by some later authors (Dzik 1986, 2000; Sansom et al. 1992; Donoghue et al. 2000, 2006) and rejected by others (Turner et al. 2010; Blieck et al. 2011). The main argument raised against such homology was the lack of any internal inclusions within the conodont basal body tissue (although structures at least remotely resembling dentine tubuli occur in some conodonts (Dzik 1986; Andres 1988). The presence of a compact lamellar tissue indistinguishable from the „euconodont" basal body tissue in one of the oldest known vertebrates removes this obstacle. It may be also of importance that the high conical cusps in the new Siberian scales are similar in size and shape to underived conodont elements.

Basally secreted hypermineralised tissue is restricted to a small group of early agnathans (possibly also chondrichthyans) but is a typical feature of conodonts (including "paraconodonts"). This is especially apparent if morphologically simple conodont elements with a thin crown tissue cover are considered. Such

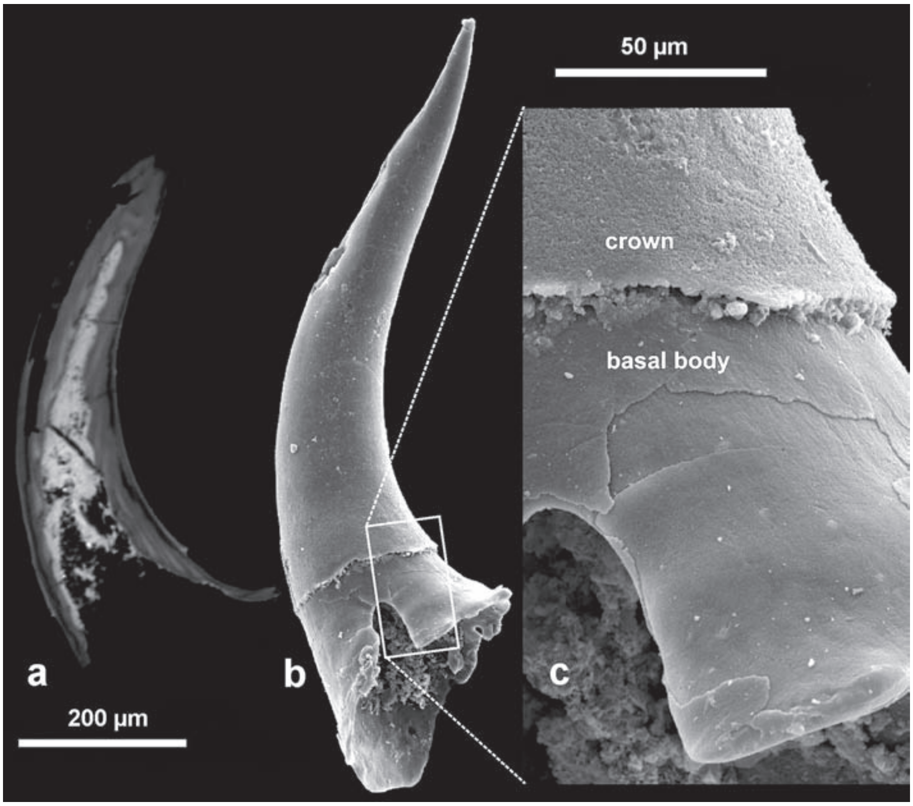

**Fig. 4.** Structure of one of the oldest euconodonts *Problematoconites* (or *Proconodontus*) sp. from the Late Cambrian *Peltura scarabeoides* Zone; glacial erratic boulder E-347 of Baltic origin collected at Chłapowo, Pomerania. **a** – X-ray microtomographic longitudinal section. **b, c** – SEM external views.

elements are known beginning from the Late Cambrian (Szaniawski & Bengtson 1998). As in other "euconodonts", their basal (pulp) cavity is filled with a layered or spherulitic phosphatic tissue indistinguishable from the agnathan lamellin (Dong et al. 2005; Dzik 2009). The main histological difference between the conodont elements and the Siberian scales is that in conodonts at least a thin layer of tissue secreted from outside is also developed (Fig. 4). If there is a homology between the agnathan lamellin and the "euconodont" basal body tissue, two possible scenarios of evolution can be considered: either the conodont crown tissue and vertebrate enamel developed independently and lack homology (Turner et al. 2010; Murdock et al. 2013) or the secretion activity by ameloblasts ceased in some early agnathans, to be restored in others (Kawasaki et al. 2005), which implies homology at least between the epithelium secreting these mineral tissues.

The decisive test for these scenarios would be to find a transitional form between the new Siberian scale and "euconodonts", having both the lamellin inside the pulp cavity and the enamel (crown tissue) outside. Such status has been already recognised in the *Conopiscius*-like fossils from the Devonian (Dzik 2009), but they can hardly be directly related to agnathans because of too late geological age (almost a hundred million years younger than the oldest agnathans) and oral location of elements in *Conopiscius* (Briggs & Clarkson 1987).

The crucial information regarding homology of tissues between the Cambrian westergaardodinid conodonts ("paraconodonts") and typical conodonts ("euconodonts") is offered by the elements transitional between the earliest unquestionable euconodont *Proconodontus* and the "paraconodont" *Problematoconites* (Fig. 4; Andres 1988; Murdock et al. 2013). Its elements are built of typically "paraconodont" tissue, rhythmically secreted from the base and perforated in its exposed portion, and a very thin cover of strongly mineralised crown tissue secreted from outside. The crown tissue dominated in advanced conodonts; the basal body frequently remained unmineralised. If agnathans are related to them, their ancestry is within "euconodonts" with a well-mineralised basal body tissue and laminar crown tissue secreted over the whole external surface of the element. Which of the element histology is ancestral for conodonts is a separate unsolved question (Bengtson 1976; Dzik 2000; Murdock et al. 2013).

## 6. Conclusions

### 6.1. Identity of Siberian scales

Because of ancient geological age of the scales from the Mamyry Formation of the Irkutsk Basin, their morphological, as well as histological simplicity seem to be plesiomorphic at least for the Siberian tesakoviaspidids. This may be used to support the hypothesis of homology between agnathan skeletal tissues and those of conodonts, the only other possible vertebrates with phosphatic skeleton predating the agnathans. The cusps and the body of the Siberian scales, built exclusively of atubular dentine (lamellin), are indistinguishable structurally from the conodont basal body tissue. However, there is little doubt that the Siberian scales covered the fish body, whereas conodont elements were parts of a complex oral apparatus. The hypothesis of homology requires migration of skeletal units from the mouth to the body surface and complete transformation of the mouth region, with loss of its grasping function. Perhaps this has something to do with ecological adaptation of the earliest agnathans to a near-shore marine environment with high organic productivity, of which the Siberian Mamyry Formation is one more example. Moreover, in conodont elements, denticles are almost always arranged in single rows, with new cusps added at ends of the processes. The serial V-shaped units with cusps characteristic of the Siberian scales do not occur in conodonts. Fossils of morphology transitional between conodont elements and fish scales remain unknown.

### 6.2. Taxonomic nomenclature

The new Siberian scales apparently represent the geologically oldest member of the tesakoviaspidids. They differ from typical tesakoviaspidids in lacking any lamellar basal layer containing Sharpey's Fibres and having cusps (odontodes) accreted onto a conical early growth stage, instead of areal-type growth and as such deserve to be a basis for at least a new species and genus. It is tentatively associated with the tesakoviaspidids.

?Family Tesakoviaspididae Karatajute-Talimaa & Smith, 2004

Genus *Kodinskaspis* nov.

**Etymology:** After the name of the Siberian city Kodinsk, close to the type locality, and Greek *aspis* (ἀσπίς) – a shield.

**Type species:** *Kodinskaspis angarensis* gen. et sp. nov.

**Diagnosis:** As for the species.

*Kodinskaspis angarensis* sp. nov.
Figs. 1-3

1984 Gen. et sp. indet (skopleniye "zubchikov"). – Moskalenko, egz. 614/243.

**Etymology:** After the Angara River.

**Holotype:** ZPAL c.XXII/49 (Fig. 1A).

**Type horizon and locality:** Left bank of the Angara River near Kodinsk upstream of Verkhnaya Kezhma Creek, where formerly the village Rozhkovka was located. Sample Angara 791-19-2; Lower Mamyry Formation.

**Diagnosis:** Conical scales composed exclusively of atubular dentine (lamellin) ornamented with cusps (odontodes) arranged in V-shaped rows sequentially added at the anterior margin during growth.

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