

Silurian cyathaspidid heterostracans of Northern Eurasia

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Received 8 April 2019, accepted 18 June 2019, available online 13 August 2019

Abstract. Silurian cyathaspidid heterostracans discovered from the East Baltic, North Timan, the Central and Southern Urals, and the Novaya Zemlya and Severnaya Zemlya archipelagoes in 1970–2006 were studied. Earlier known taxa *Archegonaspis schmidti* (Geinitz, 1884), *Archegonaspis lindstroemi* Kiaer, 1932, *Archegonaspis integra* (Kunth, 1872) and *Tolypelepis undulata* Pander, 1856 were identified and described. *Archegonaspis bimarisi* Novitskaya, 1970 is synonymized under *A. schmidti* (Geinitz) and *Tolypelepis mielnikensis* Dec, 2015 under *Tolypelepis undulata* Pander, 1856. Three new taxa, *Archegonaspis bashkirica* sp. nov., *Cyathaspis alexanderi* sp. nov. and *Tolypelepis bedovensisi* sp. nov., were established, while two taxa, *Archegonaspis lindstroemi*? Kiaer and *Tolypelepis* sp. indet., remained in open nomenclature. The new subfamily Archegonaspidae subfam. nov. was created. It is shown that besides details of the morphology of shields and plates, sculpture characteristics can be utilized in taxonomy. The material described complements the taxonomic content as well as the spatio-temporal distribution data of the species of the family Cyathaspididae.

Key words: Heterostraci, Cyathaspididae, Wenlock, Ludlow, Pridoli, Silurian, Northern Eurasia.

INTRODUCTION

Cyathaspidid heterostracans were geographically widely distributed in the Silurian of North America (e.g. Dineley & Loeffler 1976; Loeffler & Jones 1977; Soehn & Wilson 1990; Elliott et al. 1998; Elliott 2014) but also spread to Northern Eurasia (Fig. 1). Well-preserved head shields from this region have been

described by Rohon (1893: Saaremaa Island, Estonia), Kiaer (1932: Gotland Island, Sweden), Novitskaya (1970: Vaigach Island), Märss (1977a, 1977b: East Baltic – Estonia, Latvia, Lithuania and Kaliningrad District) and Dec (2015: eastern Poland). Some cyathaspidids are known from Silurian erratic boulders in northern Germany and Poland (Kunth 1872; Geinitz 1884).

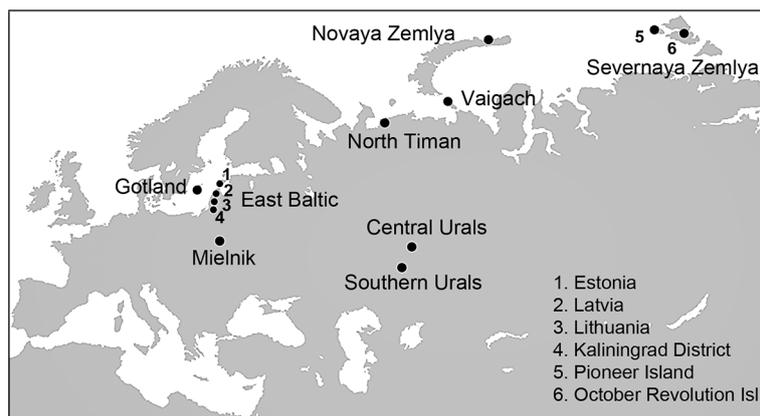


Fig. 1. Locations of Silurian cyathaspidids in Northern Eurasia: the East Baltic (1, Estonia; 2, Latvia; 3, Lithuania; 4, Kaliningrad District); Gotland Island, Sweden; Mielnik, East Poland; North Timan, Vaigach Island, Northern Island of the Novaya Zemlya Archipelago, the Central Urals, the Southern Urals, Severnaya Zemlya Archipelago (5, Pioneer Island; 6, October Revolution Island), Russia. Vector graphics from the internet.

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New material for this study was obtained in 1970–2006 from drill cores from Estonia, Latvia and Lithuania, as well as from outcrops in Estonia, the Central Urals, North Timan, Novaya Zemlya and Severnaya Zemlya. The new specimens belong to the genera *Archegonaspis* Jaekel, 1927, *Tolypelepis* Pander, 1856 and *Cyathaspis* Lankester, 1865. The specimens from the Belaya River Basin, west of the Southern Urals, characterized and depicted by Obruchev (1938), were re-described. *Archegonaspis schmidti*, *A. integra* and *A. lindstroemi* type specimens were not directly studied but their earlier published images were used.

In earlier studies, when identifying a taxon, special attention was paid to the morphology and measurements of the dorsal and/or ventral shields and smaller plates and the density of the dentine ridges covering the plates. The ridge pattern, the sculpture, was often overlooked. As perfectly complete shields are rare but the features of the sculpture and its varieties are usually available, the focus of the present work is on the sculpture. Thus, the aim of this paper is to describe the morphology of recently discovered plates and the sculpture details of specimens to find reliable features that could be used for the identification of taxa.

MATERIAL, LOCALITY AND STRATIGRAPHIC DATA

The East Baltic (Estonia, Latvia, Lithuania and Kaliningrad District)

Archegonaspis schmidti (Geinitz, 1884), established from the Lower Ludlow erratics of North Germany, was later found at a depth of 597.3 m, Ludlow, upper Silurian, in the Edole-61 core of Latvia (Fig. 1: 2), and at a depth of 1535.0 m in core No. 1 of the Kaliningrad District (Fig. 1: 4), in the Birštonas Beds, which in Lithuania correspond to the Homerian, Upper Wenlock (Radzevičius et al. 2014). A big head shield fragment of *Archegonaspis* sp. A was obtained from dark grey argillaceous limestones at a depth of 594.1 m in the Edole-61 core (Märss 1977a). Both specimens were collected by L. Hints in 1970.

Specimen GIT 721-1 of *Archegonaspis*, which was previously undescribed, was discovered at a depth of 8.9 m in the Reo-927 core (Saaremaa Island, Fig. 1: 1), in the Tahula Beds of the Kuressaare Stage, in greenish-grey limestone with argillaceous thin interlayers containing lingulid shell fragments. These beds correspond to the *Thelodus sculptilis* vertebrate Zone and the *Ozarkodina remscheidensis baccata*–*Ozarkodina snajdri parasnajdri* conodont Zone (Upper Ludfordian, Ludlow; Märss & Männik 2013). The shield was uncovered

by R. Einasto in 1991. Another new specimen of *Archegonaspis* (GIT 721-2) was retrieved from a depth of 1037.2–1037.4 m in the Girdžiai-37 core of Lithuania (Fig. 1: 3) (Pagegiai Formation, Upper Ludlow, upper Silurian) (the age determination given in the field notes of H. Nestor, Tallinn, in 1977). The sedimentary rocks of that interval are characterized as bioclastic floatstones rich in ostracode fossils. The specimen was collected by V. Viira in 1979.

The first articulated dorsal shield of *Tolypelepis undulata* Pander, 1856 was found by F. Schmidt in 1892 and handed over to V. Rohon for description (Rohon 1893; Schmidt 1893). The specimen was obtained from the Ohesaare Cliff (Saaremaa, Estonia) from the level interpreted today as the Ohesaare Stage (upper Pridoli). Another well-preserved specimen from the same locality was first illustrated by Kiaer (1932) and later repeatedly illustrated by many authors. Large fragments of both the dorsal and ventral shields of *T. undulata* have also been found at depths of 176.1 and 176.2 m in the Ruhnu core from the same stratigraphical level as in the type locality (Märss 1977b). The anterior part of the ventral shield of that taxon was described from the 401.8 m depth in the Butkunai core of Lithuania, from the undivided Minija and Jura beds (Pridoli, upper Silurian) (Märss 1977b).

Occasionally, new specimens of *T. undulata* have been found in the East Baltic. Two of them (TUG 68-1 and TUG 1384-13) originate from argillaceous semi-nodular limestones of the Ohesaare Cliff (found by T. Pani in 1987 and O. Vinn in 2006, respectively). A large fragment of a *T. undulata* dorsal shield (GIT 721-3) was luckily drilled out from calcareous dolomitic marls at a depth of 162.5 m in the Kolka-54 core, Latvia (Ohesaare Stage, upper Pridoli). That specimen was found by L. Lyarskaya in the 1970s.

The Central and Southern Urals

In 1983, A. Zhivkovich and P. Chekhovich, Moscow, found a few plate fragments of cyathaspidid heterostracans from the Silurian of the western slope of the Central Urals (Fig. 1). The fossils occurred in scattered bedrock blocks, which cropped out along the right bank of the Ufa River (a tributary of the Belaya River), downstream from the mouth of the Tabuska River. The Tabuska section has informally been called Vishnevaya Gora.

Extensive joint field work to the Tabuska (Vishnevaya Gora) section was organized in 1985, and participated in by geologists from St Petersburg (T. Modzalevskaya), Moscow (A. Zhivkovich, P. Chekhovich) and Tallinn (T. Märss). The outcrops turned out to be rich in many

Silurian vertebrate taxa including the thelodonts *Thelodus parvidens* Agassiz and *Thelodus sculptilis* Gross, cyathaspidid heterostracans, earlier identified as *Archegonaspis* sp. and possibly *Tolypelepis*, the anaspids *Schidiosteus mustelensis* Pander, *Septentrionia mucronata?* Blom et al. and *Liivilepis curvata* Blom et al., rare unidentified osteostracans, the acanthodians *Poracanthodes porosus* Brotzen and *Nostolepis striata* Pander, and the osteichthyan *Andreolepis petri* (Märss 2001, p. 178). Tabuska is the type locality of the last taxon. Apart from *A. petri*, the Silurian fishes of the Central Urals have not yet been properly described. However, a study on the distribution of vertebrates in the Pridoli and Silurian–Devonian boundary beds in Europe briefly discussed the occurrences of thelodonts and acanthodians in the northern bank of the Mikhailovsk Pond section (Märss 1997).

Cyathaspidid heterostracans have been found in four localities of the Tabuska section (*Cyathaspis* and *Archegonaspis* from localities 85-042 and 85-146-5D; *Archegonaspis* from localities 83-146-5 and 85-047). The collection contains shield fragments and scales of variable size, 35 of which have been used for this study. A few specimens with fine tessera-like units, somewhat similar to *Tolypelepis*, occur together with *Cyathaspis* (which may also have tessera-like units) in localities 85-042 and 83-146-5D. They have not yet been named due to scanty material (for details see below).

The sedimentary rocks in the Tabuska section are dark grey and pyritized, thin- to medium-bedded limestones with argillaceous shale intercalations, overlain by dark grey lithoclastic limestones. They constitute the Tabuska Beds corresponding either to the lower Pridoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow (Modzalevskaya & Märss 1991). Märss (2001) left the age, upper Ludlow or lower Pridoli, open. The level with fishes in the Tabuska Beds in the Tabuska (Vishnevaya Gora) section may be stratigraphically rather high in the Ludlow as *Andreolepis hedei* is here replaced by *A. petri* co-occurring with the zonal taxon *Thelodus sculptilis* in these rocks (Märss & Männik 2013).

Cyathaspis sp. ind. and two *Cyathaspis?* sp. specimens were collected by A. Blokhin in the early 20th century in another Belaya River section, but in the Southern Urals (Fig. 1), on the right bank of the Sirengupan River, near the village of Irgizla (latitude 52°58'11"N, longitude 57°01'11"E by Google), from localities Nos 1944 and 2769. The specimens were identified and described by Obruchev (1938, pp. 37–38), who considered them of Ludlow age. The specimens are re-described and the taxonomic affiliation of specimens is reconsidered below.

North Timan

A *Tolypelepis* shield fragment GIT 721-4 together with many smaller fragments was picked up by A. Poleshchuk in 1978 from the red sandstones of the Pridoli, Greben' Stage, at a depth of 79.8 m in the Velikaya River-81 core, North Timan (Fig. 1). The acetic acid-treated samples from depths of 78.0 and 78.8 m in the Velikaya River-81 core and from depths of 317.8 and 347.5 m in the Velikaya River-385 core, Eptarma Beds, are rich in fragments of *Tolypelepis undulata* and *Oniscolepis dentata* Pander. The thelodont *Trimerolepis timanica* (Karatajūtė-Talimaa, 1970) may occur together with them and indicate the uppermost Pridoli, upper Silurian, level. The characteristic rocks of the Eptarma Beds in the Velikaya River-385 core are argillites, siltstones and sandstones (Valiukevičius et al. 1983, fig. 3).

Novitskaya (2004, p. 104) assigned *Tolypelepis timanica* Kossovoy & Obruchev, 1962 (nomen nudum; the name just occurred in the list of fauna) from the Velikaya River outcrop, Eptarma Beds, to *T. undulata* and gave the age of the beds as Pridoli, late Silurian. This material is available in the Paleontological Institute (PIN) collections in Moscow.

The Novaya Zemlya Archipelago

The Ural Mountains continue northwards into Vaigach Island and the Novaya Zemlya islands where bedrock has yielded Silurian fishes. A large shield fragment (GIT 721-5) was collected by R. Sobolevskaya in 1988 from locality 8825-11/15a at the Right Anuchin River, Cape Vize, Severnyj (Northern) Island of Novaya Zemlya, in the uppermost part of the Konstantin Formation (Pridoli, upper Silurian) (Fig. 1). The brachiopod zonal form *Howellella pseudogibbosa* Nikiforova and several other brachiopods were identified by T. Modzalevskaya below the level with the vertebrate fragment, at locality 8825-9/3a, and correlated with the Greben' Stage in the Urals (letter by R. Sobolevskaya in January 2018). The Greben' Stage has been established in the Upper Silurian of the Urals and is marked by the *Collarothyris canaliculata* brachiopod Zone in the upper part of the Ludfordian, upper Ludlow and Pridoli (Modzalevskaya & Märss 1991; Antoshkina 2000).

Other cyathaspidid locations in Northern Europe

Some published materials on cyathaspidids are used in this work (Fig. 1). These include *Archegonaspis lindstroemi* Kiaer, 1932 from the Lau canal, Gotland Island (Hemse Beds, Ludlow; Lindström 1895; Kiaer

1932), *Tolypelepis mielnikensis* Dec, 2015 from the Mielnik core, East Poland (Přidoli; Dec 2015; for the status of the species see below), and *Archegonaspis bimariss* Novitskaya, 1970 from the northern coast of Vaigach Island, Russia (Ludlow, upper Silurian; Novitskaya 1970; for the status of the species see below).

The Severnaya Zemlya Archipelago (Pioneer Island and October Revolution Island)

A broken branchial plate of *Archegonaspis* (GIT 721-6), possibly of Wenlock age, was discovered by E. Lenkin in 1974 from Pioneer Island at locality 2055-5v (Karatajūtė-Talimaa & Märss 2002; Männik 2002; Männik et al. 2002) (Fig. 1: 5). In addition, acetic acid treatment of rocks revealed small fragments of Cyathaspididae gen. ind. also at locality 2463 of the same island.

A new *Tolypelepis* specimen (GIT 721-7) was collected by A. Khapilin in 1977 from the Bedovaya River section, October Revolution Island, from the red beds of the tripartite upper Silurian Krasnaya Bukhta Formation (Fig. 1: 6). *Tolypelepis* was collected from the lowermost part (horizon), in about the middle of 300–350 m thick cerise argillites. The argillites contained silt and 0.5–1.0 m thick interlayers of fine-grained sandstones, thin interlayers of grey argillaceous limestones (data of Khapilin & Markovskij in Matukhin et al. 1999, p. 33).

Small fragments of Cyathaspididae come from the Matusевич River section (loc. 5-2-2k, Ust' Spokojnaya Formation, Ludlow, upper Silurian) and Spokojnaya River section (loc. MF 165-1, Lower Devonian). These specimens are not included in this study.

Repositories

The collections of vertebrates marked by the combination of letters and numbers GIT 721 and GIT 408 + specimen number are housed in the Department of Geology, Tallinn University of Technology; the specimens labelled as TUG + the specimen number are the property of the Geological Museum of the Natural History Museum, University of Tartu. The specimens prefixed with LIG are curated at the Lithuanian Institute of Geology and Geography, Vilnius. Obruchev's specimens 4650-1 to 4650-3 are kept in the Central Scientific Research Geological Museum, St Petersburg.

METHODS AND TERMINOLOGY

Due to the fragmentary nature of the material, no ratios were calculated. The maximum size and the number of ridges per mm were measured in each fragment.

The terminology on the shield construction of Cyathaspidiformes is mainly based on the publications by Denison (1964), Dineley & Loeffler (1976), Märss (1977a, 1977b), Soehn & Wilson (1990), Novitskaya (2004) and Blicek et al. (2018). However, it is not clear what terms should be used when describing dentine ridge patterns in *Cyathaspis* and *Tolypelepis*. The two most discussed terms are the 'tessera-like' and 'scale-like' units. According to Denison (1964, p. 316), 'in some genera the ridges are arranged in scale-like areas that presumably represent fused scales of an ancestral condition'. Dineley & Loeffler (1976, p. 53) described the dorsal shield of *Tolypelepis* built from fused scales as scale-like units, with narrower and lower ridges arranged around a broader and higher central ridge. The scale-like units mentioned by Soehn & Wilson (1990, pp. 406, 408) are composed of mostly short and medially elliptical dentine ridges; the central ridges of units are broader and higher than those on the sides of the flanking ridges. Blicek & Karatajūtė-Talimaa (2001, p. 646) call the sculpture ridge groupings tesseriform units if they are fused together by their basal lamellar layer; such units are composed of rather wide longitudinal dentine ridges. Blicek et al. (2018, pp. 280–283) thoroughly discussed the history of formation, differences and essence of terms on dermal structures of ostracoderms: 'Tesserae are small plates of dermal bony armour of fossil ostracoderms (and gnathostomes); they are independent of other bony dermal elements, being unfused with their surrounding tesserae, platelets or plates (*sensu* Dineley & Loeffler 1976, Francillon-Vieillot et al. 1990). They are distinguished from scales of the trunk and tail by the absence of overlapping areas'. If the distinction is unclear, they propose to call the dermal bony superficial structures 'tesseriform units'. The terms 'tessera-like' and 'scale-like' just characterize the superficial ridged/tuberculated layer.

The scale-like units described in the present study have a higher medial ridge, which may be surrounded anteriorly by nearly transverse and laterally by longitudinal lower and shorter ridges. The posterior points of ridges in these units may have a narrow/short overlapping area. The units do not occur in distinct diagonal rows, for example, in *Tolypelepis* and *Cyathaspis*. The tessera-like (= tesseriform) units have short crosswise ridges also posteriorly, which partly or completely enclose the longitudinally placed ridges. The ridges in tessera-like and scale-like units have a common basal plate and unlike true scales and tesserae, are not separated from each other.

The ridge margins may carry slanting or crosswise microridges. The occurrence and shape of microridges depend on where the ridges under observation are situated on the shield.

SYSTEMATIC PALAEONTOLOGY

Class AGNATHA Cope, 1889
 Subclass HETEROSTRACI Lankester, 1868
 Order CYATHASPIDIFORMES Berg, 1937
 Family CYATHASPIDIDAE Kiaer, 1932

Diagnosis. Dorsal shield, ventral shield, paired branchial, oral, lateral and suborbital plates present; single branchial opening on each side. Dorsal shield divided into four distinct epitega. Body behind the shields covered by scales. Lateral line canals open to surface by pores arranged in longitudinal rows on dorsal and ventral shields and short transverse commissures (Denison 1964, pp. 350–351, adapted).

Subfamily ARCHEGONASPIDINAE subfam. nov.

Type genus. *Archegonaspis* Jaekel, 1927.

Content. *Archegonaspis* Jaekel, 1927.

Diagnosis. Lines between central and lateral epitega of dorsal shield do not reach shield posterior margin; median rostral process absent; preorbital processes well developed; postbranchial lobes weak; postrostral field present; posterior shield margin straight or with a jutting out median scale-like unit; anterior margin of ventral shield transverse, slightly convex or concave; simple single elongate branchial plate on both sides; medium to long longitudinal ridges run along the shields and plates excluding their foreparts (rostral epitegum, postrostral field, anterior of ventral shield and branchial plate); lateral line system dorsally expressed by pores of supraorbital canals, lateral and medial dorsal canals and dorsal transverse commissures, and ventrally by pores of postoral canals, lateral and medial ventral canals and lateral and medial ventral transverse commissures; one pair of pores anteriorly across the branchial plate.

Genus *Archegonaspis* Jaekel, 1927

Synonymy. See Novitskaya (2004, p. 101).

Type species. *Cyathaspis integer* Kunth, 1872.

Species content. *Archegonaspis integra* (Kunth, 1872); *A. schmidtii* (Geinitz, 1884) including *Archegonaspis bimariss* Novitskaya, 1970; *A. lindstroemi* Kiaer, 1932 including *Archegonaspis* sp. A Märss, 1977a; *Archegonaspis bashkirica* sp. nov.; *Archegonaspis* sp. cf. *A. schmidtii* and four types of ?*Archegonaspis* sp. ind. (Dineley & Loeffler 1976; Loeffler & Jones 1976). Affiliation of *A. ludensis* (Salter, 1859) and *Archegonaspis* sp. (White, 1958) from England to *Archegonaspis* is still

not firmly established (Denison 1964; Märss 1977a; Novitskaya 2004). *Archegonaspis* sp. B, assembling together many microremains from the drill cores (Märss 1977a), will remain in open nomenclature.

Occurrence. Estonia, Latvia, Lithuania and Kaliningrad District, East Baltic, Upper Wenlock? and Ludlow; Gotland Island, Sweden, Ludlow; erratic boulders of northern Germany and Poland corresponding to the Ludlow; Pioneer Island, Wenlock; Vaigach Island, Upper Ludlow; the Central Urals, Russia, Upper Ludlow or lower Pridoli, upper Silurian; Southern Urals, Bashkiria, Russia, Ludlow; Northwest Territories of Canada, upper Silurian or Lower Devonian.

Diagnosis. Dorsal shield length 38–47 mm; epitega distinct; ridges medium to long; ridge pattern transverse on rostral epitegum, elliptical or longitudinal on central epitegum and longitudinal on lateral epitega; postrostral field distinct with fan-shaped or irregular ridge pattern; ventral shield with longitudinal ridges and with anterior triangular area of fanned or irregularly distributed ridges or denticles; dentine ridge density 4–6, in some cases 6–8 ridges per mm; pores of lateral line canals medium to small in diameter (Denison 1964; Novitskaya 1970, 2004, adapted herein).

Archegonaspis schmidtii (Geinitz, 1884)

Figure 2A–E

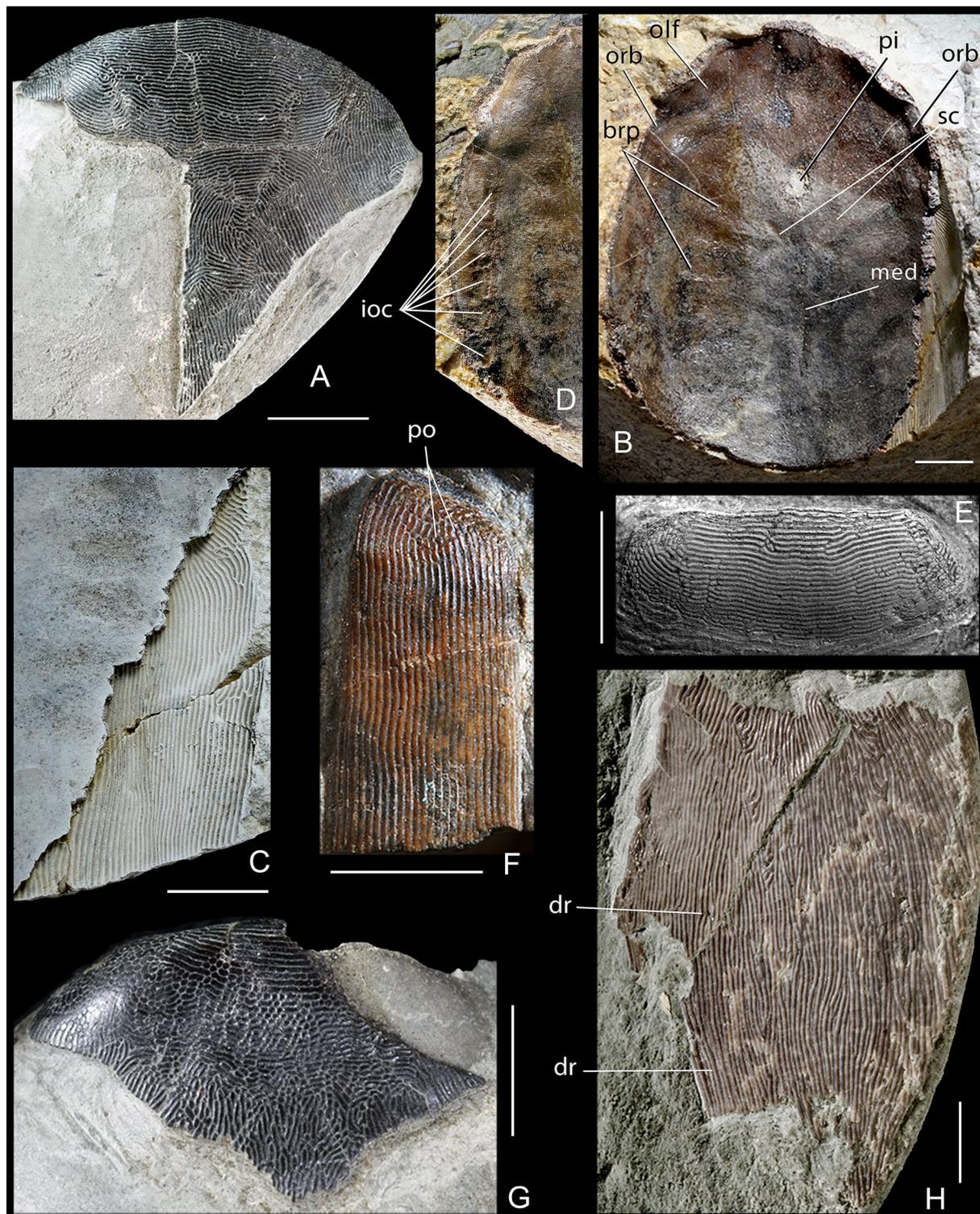
- 1884 *Cyathaspis schmidtii* Geinitz; pp. 854–857, pl. 30, figs 1, 2.
 1932 *Archegonaspis integer* var. *schmidtii* Geinitz; Kiaer, p. 24.
 1958 *Aequiarcheponaspis schmidtii* Stensiö; p. 307, fig. 174.
 1964 *Archegonaspis schmidtii* (Geinitz); Denison, pp. 365–366, fig. 113.
 1970 *Archegonaspis bimariss* Novitskaya; pp. 105–113, pl. 10, figs 1, 2, text-figs 3, 4; Novitskaya 2004, p. 102, pl. 1, figs 1, 2, text-fig. 12a.
 1977a *Archegonaspis schmidtii* (Geinitz); Märss pp. 130–131, figs 1A, B; 2B, C; 3A, B; pl., figs 1, 2.

Holotype. Dorsal shield in Geinitz (1884, pl. 30), collection number GG 489/ 1, University of Greifswald. The description of *Archegonaspis schmidtii* (Geinitz) was based on the only specimen, which obtained the status of the holotype fixed by monotypy (ICZN 1999, Art.73.1.2).

Remarks. Denison (1964, p. 366, fide Woodward 1891) gave The Rostock University Museum as the location of the holotype. Our inquiry addressed to the Rostock

University (e-mail of 20.03.2019) resulted in the reply that they were not aware of that fish. Recently (in June 2019) a successful effort was made by Thomas Mörs, Swedish Museum of Natural History, who found the specimen and clarified the new repository of the

holotype. It is housed now in the palaeontological type collection of the geological collections of the Institute for Geography and Geology, University of Greifswald, with the number GG 489/ 1 (GG = Geology Greifswald, 489 refers to the publication).



Type locality and horizon. Glacial erratics of Graptolithengestein, near Rostock, North Germany, upper Silurian (Denison 1964).

Material. GIT 171-1 (= Pi 5027), depth 597.3 m, Edole-61 core, Latvia, Ludlow; LIG 25-022, depth 1535 m, core No. 1, Kaliningrad District, Birštonas Beds, Upper Wenlock; GIT 721-2, depth 1037.2–1037.4 m, Girdžiai-37 core, Lithuania, Pagegiai Formation, Upper Ludlow, upper Silurian.

Occurrence. Upper Wenlock and Ludlow of the East Baltic, Ludlow of Vaigach Island, Russia, and glacial erratics of North Germany.

Diagnosis. Dorsal shield elongate oval with length slightly more than 42 mm and width 23 mm; anterior edge notably convex; rostral epitegum with transverse ridges, which on sides turn to anterior; central epitegum generally longitudinally ridged with medium to long uniform convex ridges; transverse ridges anteriorly on postrostral field combined with arch-like ridges posteriorly of that field; lateral epitega longitudinally ridged (Geinitz 1884, p. 855, amended).

Remark. Denison (1964, p. 366) diagnosed *A. schmidti* as having the dorsal shield 38 mm long, which is less than the value given by Geinitz.

Description. For the completeness of data, we reproduce here the figures of *A. schmidti* from the East Baltic published in Märss (1977a) (Fig. 2A, E). The epitega on GIT 171-1 (Fig. 2A) are distinct, separated by denticulated ridges in the groove. The dentine ridges are of uniform size in the limits of the rostral (4–5 ridges per mm) and the central epitegum (4.5 per mm), but are finer on the lateral epitegum (6 per mm). They are parallel and transverse on the main part of the rostral epitegum (Fig. 2A, E) and anteriorly on the postrostral field of the central epitegum; the ridges turn anteriorly on the sides of the rostral epitegum. They form curves

on the right side of the postrostral field (Fig. 2A, E), while the field is not distinct judging from the right half of that field. The pores of the supraorbital canal are distinct (Märss 1977a, fig. 3A, B).

The new material comes from a depth of 1037.2–1037.4 m in the Girdžiai-37 core (Lithuania, Pagegiai Formation, Upper Ludlow, upper Silurian). The drill core has entrapped a single large fragment of a cyathaspidid bony exoskeleton, specimen GIT 721-2, which we identified as the dorsal shield of *Archegonaspis schmidti* (Geinitz) in visceral view (Fig. 2B, details in Fig. 2C, D). The posterior part of it is out of the drill core perimeter, and a small piece of bone is broken off on the left lateral side exhibiting a triangular patch of the mould (Fig. 2C). The maximum length of the partial dorsal shield is 37.8 mm and width 30.9 mm. The anterior margin of the shield is rather strongly convex and gently notched due to the impact of internal organs (see below). On the basis of the imprints of the sculpture left in the mould, the measurements of dentine ridges could be taken and the exact location of the fragment on the body defined. The mould reflects the boundary (suture) between the lateral and central epitega drawn by the wedging ridges along the visible area. The average density is 4 ridges per mm. The ridges are long, of uniform shape and smoothly convex closer to the mid-shield from the suture. A few patches with short ridges occur most anteriorly of the broken edge. The lateral epitegum has sharp-crested ridges.

The visceral surface of the dorsal shield exhibits the impressions of internal organs (Fig. 2B and detail Fig. 2D). The impressions of the olfactory organ are located anteriorly on both sides of the midline; orbital notches occur somewhat posteriorly of it. On the midline a pineal impression is followed by the impressions of semicircular canals, behind which there is a long, posteriorly narrow structure, the impression of a part of the brain, the medulla; seven (eight?) elongate oval impressions of gill pouches are situated on both sides of

Fig. 2. *Archegonaspis* species from the East Baltic and Severnaya Zemlya Archipelago. **A–E**, *Archegonaspis schmidti* (Geinitz): **A**, anterior portion of the dorsal shield, the rostral, small part of central and right lateral epitega, GIT 171-1 (previous number Pi 5027, re-imaged from Märss 1977a); **B**, large anterior portion of the dorsal shield in visceral view; **C**, close-up of (B) with a small piece of bone broken off from the left lateral side exhibiting the mould of sculpture; **D**, detail of (B) with impressions of individual exhalant canals of gill pouches (note small pits at the bottom of each hollow), GIT 721-2; **E**, rostral epitegum, LIG 25-022 (re-imaged from Märss 1977a); **F**, *Archegonaspis ?lindstroemi* Kiaer: anterior part of the right branchial plate, GIT 721-6; **G**, *Archegonaspis lindstroemi* Kiaer: partial rostral epitegum and postrostral field of central epitegum, GIT 171-2 (previous collection number Pi 5028, re-imaged from Märss 1977a); **H**, *Archegonaspis integra* (Kunth): a large fragment of the dorsal mid-shield, GIT 721-1. Scale bars = 5 mm. *Locations:* A, Edole core, depth 597.3 m, Latvia, Ludlow; B–D, Girdžiai-37 core, depth 1037.2–1037.4 m, Lithuania, Pagegiai Formation, Upper Ludlow; E, No. 1 core, depth 1535 m, Kaliningrad District, Birštonas Beds, Upper Wenlock; F, locality 2055v, Pioneer Island, Severnaya Zemlya Archipelago, Wenlock; G, Edole drill core, depth 594.1 m, Latvia, Ludlow; H, Reo-927 core, depth 8.9 m, Saaremaa, Tahula Beds of Kuressaare Stage, upper Ludlow, upper Silurian. *Abbreviations* (including impressions of internal organs, mainly from Novitskaya 2004, fig. 88): brp, branchial pouches; dr, double-ridge; ioc, individual exhalant canals; med, medulla; olf, olfactory organs; orb, orbital notch; pi, pineal organ; po, pores of possible branchial transverse commissure; sc, semicircular canal (here shown are anterior ones).

the midline. A row of hollows with about 4–6 small pits at the bottom of each hollow occurs along the left side of the mould, laterally of the impressions of gill pouches (Fig. 2D). The hollows are the impressions of individual exhalent ducts of gill pouches (Novitskaya 2004, fig. 30) found also on two *Poraspis* and one *Anglaspis* species (Stensiö 1958, figs 179A, B, 180A) and on one *Listraspis* species (Denison 1964, fig. 132A). Small pits at the bottom of the hollows are shown here for the first time.

Archegonaspis lindstroemi Kiaer, 1932
 Figures 2G, 3A–G, 4A–C, E–Q

- 1895 *Cyathaspis?* *Schmidtii* Geinitz; Lindström, pp. 1–10, text-fig. 1a–c, pls 1, 2.
 1932 *Archegonaspis lindströmi* n. sp.; Kiaer, pp. 23–24, pl. 9, fig. 1.
 1933 *Archegonaspis lindströmi* Lindström; Heintz, pp. 126–127, 130–131, fig. 3.
 1958 *Lauaspis lindströmi* (Kiaer); Stensiö, p. 307, fig. 172A, B.
 1964 *Archegonaspis lindstromi* Kiaer; Denison, pp. 363–364, fig. 112.
 1977a *Archegonaspis* sp. A; Märss, pp. 131–132, text-figs 1C, 2D, 3C, pl., figs 3, 6.
 1988 *Archegonaspis lindstroemi* Kiaer; Fredholm, pp. 160–161, fig. 3A–D.

Remarks. Originally the cyathaspid specimens with an intact dorsal and posteriorly partly broken ventral shield were described by Lindström (1895) as *Cyathaspis? Schmidtii* Geinitz, with the dorsal shield handled first, followed by the descriptions of the ventral shield, a smaller plate and two scales. That smaller plate was later recognized as a branchial plate (Kiaer 1932; Heintz 1933). Kiaer (1932) had all Lindström's specimens in his possession when establishing the species *Archegonaspis lindströmi* n. sp. By referencing Lindström's description, he (ibid.) validated the name of that taxon (ICZN 1999, Article 13.1.2). However, a type was not erected nor was a species diagnosis actually provided in his work and the location of the specimens was erroneously given as Skaane, South Sweden. When referencing Lindström's description, Kiaer accepted that the original shields and plates were part of a single individual. Later, in the explanations of the figure of *Lauaspis lindströmi* (Kiaer), Stensiö (1958, fig. 172A) showed Lindström's specimen (the dorsal shield) as the holotype. The generic name *Lauaspis* was synonymized under *Archegonaspis* by Denison (1964).

According to ICZN (1999, Article 27): 'No diacritic or other mark (such as an apostrophe), or ligature of the letters *a* and *e* (*æ*) or *o* and *e* (*oe*) is to be used in a scientific name', while the authorship is fixed by IZCN

(1999, Article 19.2). Therefore the valid species name is *A. lindstroemi* introduced by Kiaer (1932).

Holotype. Dorsal shield No. C1564A (Lindström 1895, pl. 1, fig. 1); ventral shield No. C1564B (the specimen in Lindström 1895, pl. 1, fig. 5; Kiaer 1932, pl. 9, fig. 1); broken branchial plate No. C1784 (the specimen in Lindström 1895, pl. 1, figs 9–12) and two scales, No. C1782 and No. C1783 (the specimens in Lindström 1895, pl. 1, figs 6 = 7, and fig. 8, a mould of a scale). Holotype constituents are housed in the Natural History Museum, Stockholm.

Type locality and horizon. Lau canal, Lau Parish, Gotland Island, Sweden; Hemse Beds, Ludlow, upper Silurian (Fig. 1).

Material. GIT 171-2 (= Pi 5028), partial rostral epitegum and postrostral field, depth 594.1 m, Edole drill core, Latvia; GIT 408-1, right side of a broken dorsal shield; GIT 408-9, anterior part of a platelet?; GIT 408-10, postero-medial part of a dorsal shield; GIT 408-11, lateral plate, loc. 85-042; GIT 408-12, possibly the anterior part of a branchial plate; GIT 408-13, possibly the posterior part of a branchial plate, loc. 85-146-5; GIT 408-21–GIT 408-23; GIT 408-25–GIT 408-37, the scales, loc. 85-042, Tabuska (Vishnevaya Gora) section, the Central Urals, Russia.

Occurrence. Ludlow of Latvia; upper Ludlow (Modzalevskaya & Märss 1991) or lower Pridoli (Shujskij 1981; Shurygina et al. 1981), upper Silurian of the Central Urals, Russia.

Diagnosis. Dorsal shield 47 mm long and 30 mm wide at maximum; anterior margin nearly transverse; posterior margin rather straight with a short median process; orbital notches shallow; shield division into epitega very distinct; dentine ridges on rostral epitegum short and transverse, or tuberculate; ridges on central and lateral epitega longitudinal, long, of uniform size and similar width; tessera-like unit(s) may occur posteriorly on central epitegum; ridge surface on central epitegum flat or slightly convex; triangular postrostral field expressed with fan-shaped pattern of tubercles or short ridges; row of ridges near posterior end of dorsal shield forming medial short crest; ventral shield 44 mm long and 29 mm wide at maximum, anterior margin truncate with shallow medial notch; very short irregular ridges and tubercles on anterior triangular area; branchial plate narrow, elongate, gradually tapering posteriorly and ending bluntly anteriorly; plate covered with convex, longitudinally continuous (without interruptions) nearly parallel ridges, which may form a keel posteriorly [Diagnosis compiled after Lindström (1895, pp. 3–8)

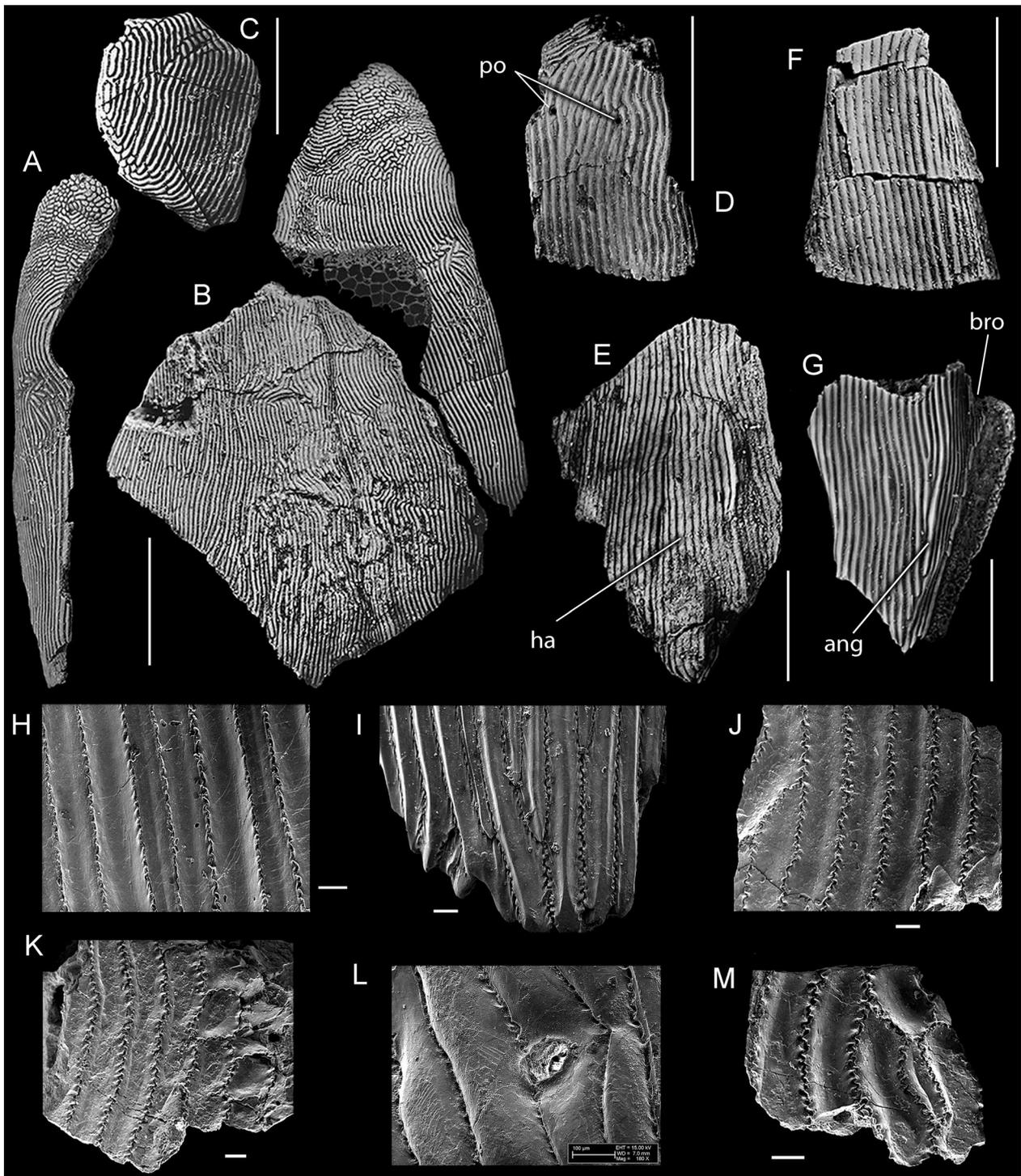


Fig. 3. A–G, *Archegonaspid lindstroemi* Kiaer from the Central Urals. A, B, broken dorsal shield in right side view (A) and in dorsal view (B), GIT 408-1; C, possibly a lateral plate, GIT 408-11; D, anterior part of a scale or platelet; pores of the lateral line canal accentuated with two black dots, GIT 408-9; E, small portion of the postero-median dorsal shield, GIT 408-10; F, possibly part of a branchial plate, GIT 408-12; G, possibly the posterior part of a branchial plate, GIT 408-13; H–M, examples of fine ridgelets at the margins of dentine ridges; H, *Archegonaspid integra* (Kunth), GIT 408-50; I, *Archegonaspid* sp., GIT 408-48; J–M, Cyathaspididae gen. et sp. indet. J, GIT 408-52; K, GIT 408-51; L, GIT 408-49; M, GIT 408-53. Scale bars = 5 mm (A, B); 3 mm (C–G); 100 μ m (H–M). *Locations*: Tabuska (Vishnevaya Gora) section, locality 85-042 for (A–I, L); locality 85-146-5D for (J, K, M); the Central Urals, Tabuska Beds either of the lower Pridoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow level (Modzalevskaya & Märss 1991). *Abbreviations*: ang, sharp angulation along the branchial plate; bro, branchial opening; ha, healed area; po, pores of lateral line canal.

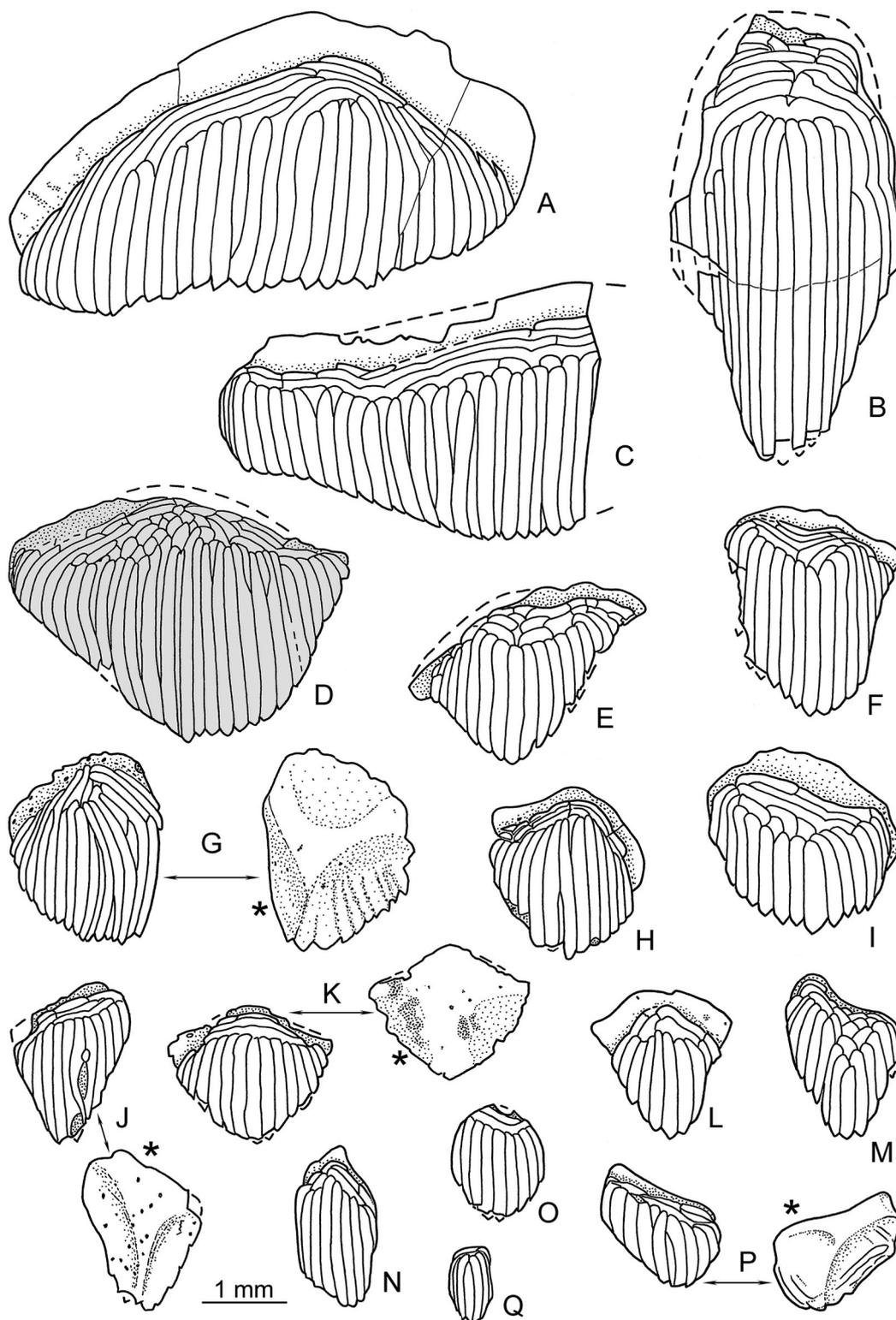


Fig. 4. *Archegonaspis lindstroemi* Kiaer: A–C, E–Q, set of scales; D, scale possibly from *A. integra* (Kunth). A, GIT 408-21; B, GIT 408-23; C, GIT 408-22; D, GIT 408-24; E, GIT 408-25; F, GIT 408-26; G, GIT 408-27; H, GIT 408-28; I, GIT 408-29; J, GIT 408-30; K, GIT 408-31; L, GIT 408-32; M, GIT 408-33; N, GIT 408-34; O, GIT 408-35; P, GIT 408-36; Q, GIT 408-37. Scale bar = 1 mm. *Location:* Tabuska (Vishnevaya Gora) section, locality 85-042, the Central Urals, Tabuska Beds either of the lower Pridoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow level (Modzalevskaya & Märss 1991). The asterisk (*) indicates the basal view of the scales connected with a line; shadow in D is for another species in the set as given above.

and Obruchev (1964, p. 57) with main stress on the sculpture herein].

Description. Specimen GIT 171-2 (Fig. 2G), the anterior part of the dorsal shield, was described earlier as *Archegonaspis* sp. A (Märss 1977a). Its dentine ridges (4 per mm on the rostrum) are divided into short lengths.

A large fragment of dorsal shield GIT 408-1 (Fig. 3A dorsal shield in side view and 3B in dorsal view) comprises a small right part of the rostral epitegum, right lateral epitegum and part of the central epitegum. The fragment is up to 26.5 mm long and 17 mm wide, while the right lateral epitegum posteriorly is a 7 mm wide stripe. The sutures between the rostral and lateral epitega and between the central and lateral epitega are slightly deeper furrows bearing short tubercles or elongate fine ridgelets. The rostral epitegum is anteriorly covered by tubercles or short ridges, which become somewhat longer and are transverse close to the central epitegum. On the central epitegum, on the left side of the fragment the ridges are relatively regularly shaped, with just a few ones merging or branching. The ridges are mainly of uniform width, interrupted and somewhat wavy. The distribution of ridges is very irregular on the posterior part of the fragment, on both sides of the suture (Fig. 3B), where the ridges can sporadically be shorter and meandering. The right lateral epitegum is rather well preserved (Fig. 3A, B). The short ridges on the proximal part of the lateral epitegum are parallel to the suture between the rostral and lateral epitega. The right lateral view (Fig. 3A) shows the orbital notch with an eroded preorbital process and the postorbital lobe. The ridges above the orbit are very uniform in width, forming an arch-like pattern over the orbital notch before proceeding to the posterior. In the posterior part of the lateral epitegum, close to the suture with the central epitegum, the ridges become disorderly distributed.

The density of ridges is 6 per mm on the central epitegum and medially on the lateral epitegum, while above the orbit and closer to the lateral margin there are 5 ridges per mm. The ridges are round-crested on the central epitegum and medially on the lateral epitegum, while the tubercles are rather flat on the rostral epitegum, and sharp-crested behind the orbital notch. All ridges, short and long, have fine side ridgelets, indentations, which begin at the 'foot of a ridge' and run upwards. On the rostral epitegum they occur crosswise to the ridges, making the margins denticulate. Beneath the removed surface layer the vacuoles of the medial layer become exposed, the structure that is common for all cyathaspidids. Pores of the lateral line were not detected.

Specimen GIT 408-11 (Fig. 3C) is possibly a lateral plate from the antero-lateral part of the ventral side of

a fish. Its morphology is most similar to that of *Anglaspis heintzi* Heintz (Heintz 1962, fig. 7L, P) and also of *Tolypelepis undulata* Pander (Märss 1977b, fig. 6D, D1). It is asymmetrical, with a rather flat surface and the maximum diagonal measurement of 5.75 mm. No overlapped area is observed. The antero-lateral downturned margin on the left side of the image bears two short ridges, both surrounded by two crescent ridges (a kind of simple tessera-like units). Behind that structure the plate is covered with uniform, almost parallel arcuated ridges. There are 6 dentine ridges per mm in the mid-plate. The margins of the ridges are finely denticulate.

Specimen 408-9 (Fig. 3D) is a fragment from the anterior part of a plate, with a maximum length of 4.5 mm and width of 2.9 mm. It has six oblique narrow ridges anteriorly with an intact anterior margin, and round-topped longitudinal ridges on the main area, six ridges of the same width per mm. About in the middle of the fragment, some short ridges appear between the long ones. Two lateral line canal pores, marked by black dots, seem to form a short crosswise commissure. The identification of the fragment is not sure – it might be a scale (the size fits but the crosswise lateral line does not), or a piece of the ventral? shield.

Specimen GIT 408-10 (Fig. 3E) is a small part of the postero-median dorsal shield, 9.6 mm long and 5.8 mm wide. The middle part of the fragment, which has both elongated ridges and tessera-like units, is separated from the rest of the fragment by a fissure. This patch with interrupted distribution of ridges seems to indicate a fractured and healed area of the shield. The left-side margin is of three stepwise-lengthened ridge-sets whose posterior extremities are broken off, while the posterior medial and right margins are intact. In the tessera-like median unit the higher central ridge is embraced by one to three side ridges. Two longitudinally successive units on the right side of it form the highest, asymmetrically placed part of the fragment. Outside this area the ridges are long and rather straight. The density of ridges is mainly 5 per mm but on the left side there are 8 ridges per mm; the ridges have a slanting surface rising towards the midline of the fragment, where they become flat. The fine dentation on ridge margins is recognizable. Lateral line canal pores were not noticed in this specimen.

Specimen GIT 408-12 (Fig. 3F) is most possibly a fragment of a branchial plate, at a maximum 5 mm long and 3.4 mm wide. Both of its longitudinal margins are intact but both ends are broken. The dorsal margin (the right margin in the figure) turns down at an angle of 70° and indicates an overlapped area. One to two ridges on the edge are just slightly coarser, otherwise there are 6 ridges per mm in the mid-fragment, altogether 21–22 ridges at the wider end. The ridges follow the plate dorsal margin and are parallel to it. On the opposite side

new ridges are stepwise added to the plate which also becomes wider there.

Element GIT 408-13 (Fig. 3G) is the posterior part of a left branchial plate; its anterior 2/3 and partly the posterior part (except its apex) are broken. The visceral side of the plate is flat and smooth with a maximum length of 7 mm along the edge and width of 4.8 mm. The dentine ridges on the larger and smoother surface are mostly of uniform shape, of the same width and height, with a density of 5.5 ridges per mm; a couple of ridges have a swollen segment. A number of ridges terminate on the relatively sharp edge (lateral angulation of Denison 1964, p. 319), which runs along the longer axis of the plate surface. On its narrower surface the ridges are narrower as well but still uniformly shaped. Here the ridges run parallel to the sharp edge but some of them end at the overlapped brim, a rather wide area on the dorsal side (the right side in the figure). A smoothly roundish anterior end of the overlapped brim forms the mouth of the branchial opening, a shallow and short groove directed posteriorly.

To have an idea about the set of the scales of this taxon, we sampled them strictly from one locality 85-042, Tabuska (Vishnevaya Gora) section (Fig. 4). The scales with longitudinal ridges of uniform shape have anteriorly long crosswise ridges while the longest are situated anteriorly on the scales (Fig. 4A–C). More posteriorly the crosswise ridges become shorter (Fig. 4E, H, J, M, Q) but sometimes still tend to occupy the whole width of the sculptured area of the scales (Fig. 4F, G, I, K, L, N–P). The overlapped area is longer on more anterior scales than on posterior ones. The largest scale is 6.3 mm wide and 3.3 mm long; a median mid-length scale is 5.5 mm long and 2.8 mm wide. The smallest scale is less than 1 mm long and 0.5 mm wide. Larger scales bear 5–6 ridges per mm. The visceral side of the scales has overlapping areas postero-laterally (Fig. 4G*, J*, K*, P*). One scale differs in a few features from the described ones (Fig. 4D, in grey). It has small tubercles on its anterior part instead of crosswise ridges, followed by ridges of different widths; fine intermediate ridges wedge out posteriorly. In light of these features this scale might belong to another taxon, to *A. integra* (Kunth).

Archegonaspis ?lindstroemi Kiaer, 1932
Figure 2F

A broken right branchial plate (anterior part, GIT 721-6, Fig. 2F) comes from locality 2055v on Pioneer Island, Severnaya Zemlya Archipelago, Wenlock, Silurian. The plate is just slightly convex along the midline. The maximum length of the sculptured area is 13.3 mm and maximum width 6.5 mm; the latter narrows up to

5.5 mm before ending anteriorly. The narrow anterior-most triangular area is covered with tiny tubercles and followed by short ridges; most of the plate is covered with uniform longitudinal smoothly convex to flat dentine ridges except the most ventral 2–2.5 mm of the plate (on the right in the figure) which carries sharp-crested longitudinal ridges. The density of ridges is 4 per mm. The ridged ventral margin of the plate turns down at a right angle; the upper downturned margin seems to be without ridges (or they may be worn out). The margins of ridges are smooth. Two pores of the lateral line canal are situated in 2 mm from the anterior margin near the midline. They are very fine and, as much as can be discerned from the figure, they pass through the ridges at their margins. If this is the case, they may form the branchial transverse commissure(?). The long, uniformly shaped, somewhat flattened ridges and their density on the mid-plate are in accordance with the diagnosis of *A. lindstroemi*, but as the posterior half of the plate is not available, the taxon is identified here with some doubt.

Archegonaspis integra (Kunth, 1872)
Figures 2H, 3H, 4D (with doubt), 5, 6A–E

Synonymy. See Denison (1964, p. 363).

Type species. *Cyathaspis integer* Kunth, 1872.

Holotype. MB 1975, pl. 1, figs 1–6 of Kunth (1872), the core of the specimen, the impressions of the dorsal and ventral shields, branchial plate and anterior scales, and the counterpart of the dorsal shield are all of the same individual; this is the holotype by monotypy housed in the Berlin Museum für Naturkunde.

Type locality. Beyrichienkalk; Schöneberg near Berlin, northern Germany (Kunth 1872); Early Ludlow (Denison 1964, p. 363).

Remarks. The dorsal and ventral sides of the holotype (MB 1975; Kunth 1872, pl. 1, figs 1, 3) have distinct shield morphology, but no sculpture layer is preserved. Kiaer (1932, pp. 22–23, pl. 9, fig. 2) assigned another specimen, MB.f.8031a, b (old number MB. 1975.4) from another boulder locality (Erkner, near Berlin), erroneously as geno- and holotype. Stensiö (1958, explanation to fig. 173A) did the same by illustrating the cast of the dorsal shield of that specimen and keeping its status as the holotype. Both Kiaer and Stensiö studied the gypsum or lead casts, which carry beautiful ridge patterns on the outer surface. Denison (1964, p. 363) diagnosed the sculpture as ‘On the central epitegum a few ridges stand slightly higher than the others’, possibly using the specimen figured by Kiaer (1932) or Stensiö (1958) to feature the ridges.

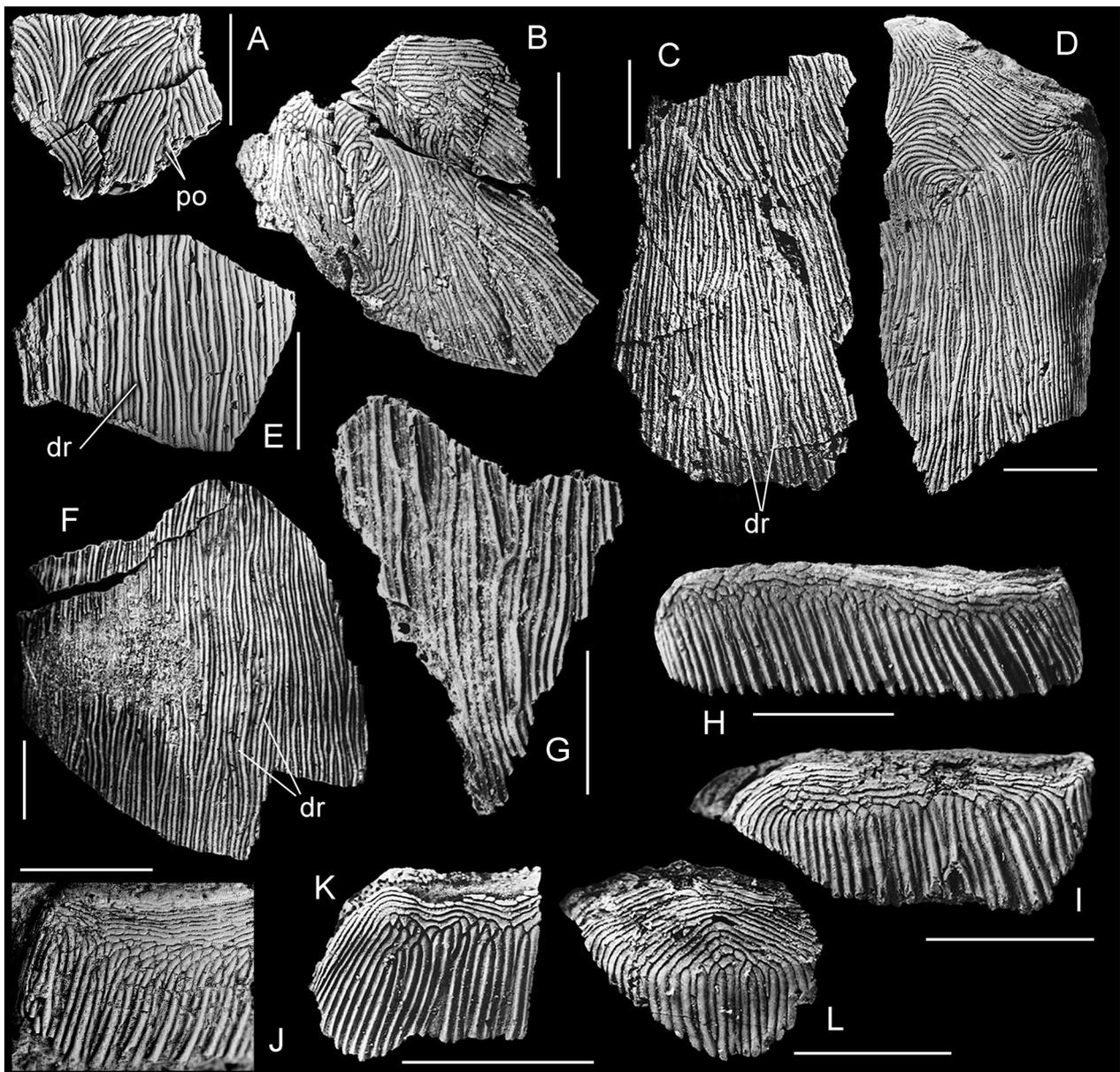


Fig. 5. *Archegonaspis integra* (Kunth): fragments of the dorsal and ventral side of the shields, and the scales: **A**, small fragment from the right side of the dorsal shield (partial rostral, central and ?lateral epitega), GIT 408-3; **B**, fragment from anteriorly of the right side of the dorsal shield, GIT 408-7; **C**, big fragment of the middle and right portions of the dorsal shield, GIT 408-6; **D**, left side of the ventral shield broken posteriorly, GIT 408-2; **E**, **F**, the position of these fragments on the body is unclear, possibly the ventral shield, GIT 408-4 and GIT 408-5, respectively; **G**, the position of the fragment on the body may be dorsal, GIT 408-8; **H–K**, dorso-lateral scales: **H**, GIT 408-39; **I**, GIT 408-41; **J**, GIT 408-38; **K**, GIT 408-40; **L**, ventro-lateral scale, GIT 408-42. Scale bars = 3 mm. *Locations*: **A–E**, **G–L**, locality 85-042; **F**, locality 85-146-5D, Tabuska (Vishnevaya Gora) section, the Central Urals, Tabuska Beds either of the lower Přidoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow level (Modzalevskaya & Märss 1991). *Abbreviations*: dr, double-ridge; po, pores of lateral line canal.

Material. GIT 721-1, a big fragment of the dorsal shield, depth 8.9 m, Reo-927 core, Saaremaa, Tahula Beds of the Kuressaare Stage; GIT 408-2, anterior and mid-portions of the left side of the ventral shield, locality 85-042; GIT 408-3, a small fragment from the right side

of the dorsal shield with a patch of the postrostral field and with a part of the supraorbital canal, locality 85-042; GIT 408-4 (locality 85-042) and GIT 408-5 (locality 85-146-5D), fragments of unclear origin on the body, possibly ventral shield based on sculptural similarities

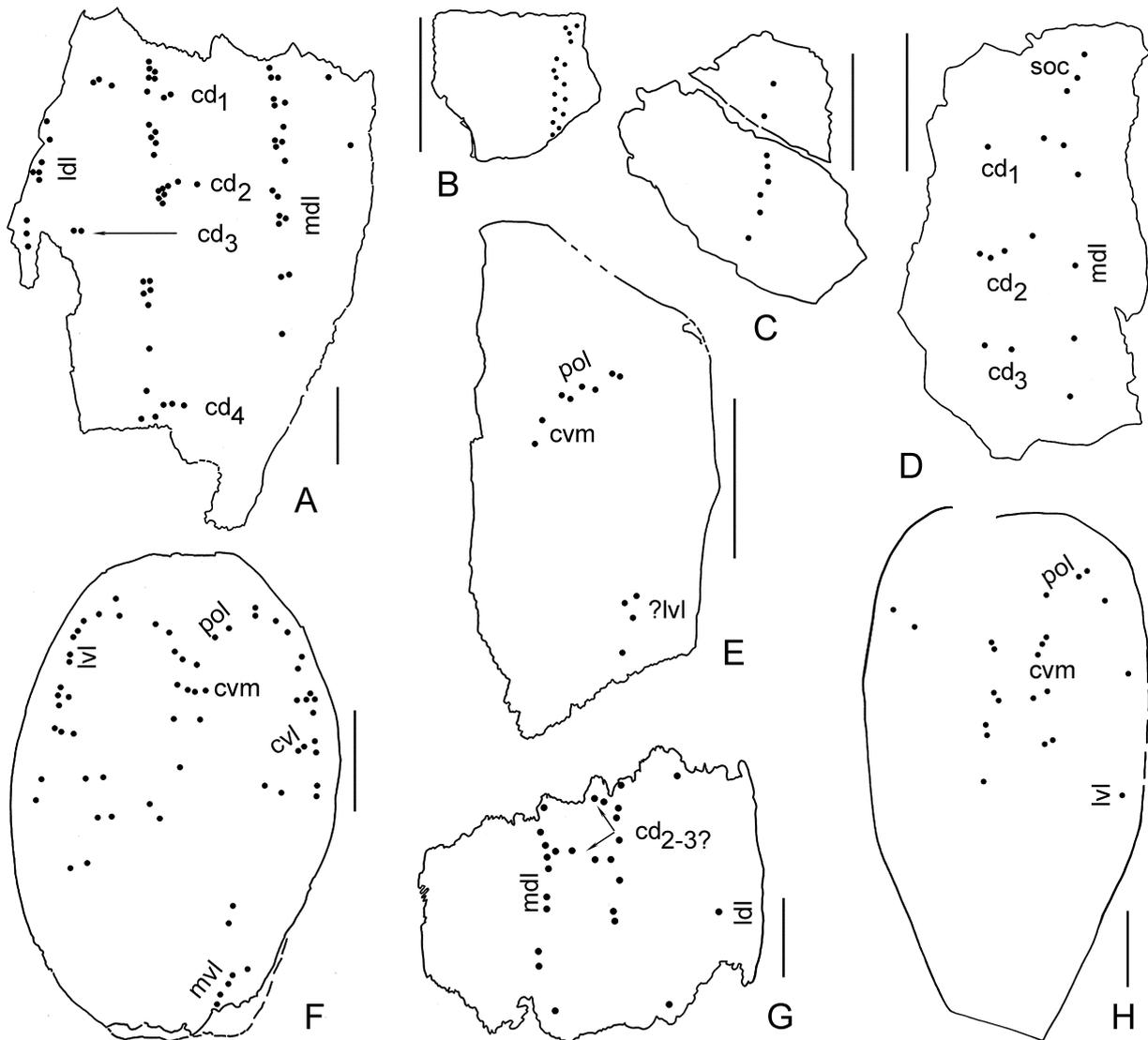


Fig. 6. Pores of lateral line canals (pores shown larger than they are in reality): **A–E**, *Archegonaspis integra* (Kunth); **F, G**, *Tolypelepis undulata* Pander; **H**, *Tolypelepis bedovensis* sp. nov. **A**, dorsal shield, GIT 721-1; **B**, dorsal shield, GIT 408-3; **C**, dorsal shield, GIT 408-7; **D**, dorsal shield, GIT 408-6; **E**, ventral shield, GIT 408-2; **F**, ventral shield, TUG 68-1; **G**, dorsal shield, GIT 721-3; **H**, ventral shield, GIT 721-7. Scale bars = 5 mm (A–E, G, H); 1 cm (F). *Locations*: **A**, Reo-927 core, depth 8.9 m, Saaremaa, Estonia, Tahula Beds of the Kuressaare Stage, upper Ludlow; **B–E**, locality 85-042, Tabuska (Vishnevaya Gora) section, the Central Urals, Tabuska Beds either of the lower Pridoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow level (Modzalevskaya & Märss 1991); **F**, Ohesaare Cliff, Saaremaa, Estonia; **G**, Kolka-54 core, depth 162.5 m, Latvia, Ohesaare Stage, upper Pridoli; **H**, Bedovaya River section, October Revolution Island, Severnaya Zemlya Archipelago, Krasnaya Bukhta Formation, upper Pridoli, upper Silurian. *Abbreviations* (following Denison 1964): cd₁₋₄, first to fourth dorsal transverse commissures cvl, lateral ventral transverse commissure; cvm, medial ventral transverse commissure; ldl, lateral dorsal canal; lvl, lateral ventral canal; mdl, medial dorsal canal; mvl, medial ventral canal; pol, postoral canal; soc, supraorbital canal.

with GIT 408-2; GIT 408-6, a big fragment of the medial and right part of the dorsal shield, locality 85-042; GIT 408-7, a fragment from the anterior right side of the dorsal shield, locality 85-042; GIT 408-8, the position of this fragment may be dorsal judging from the more complicated sculpture like in GIT 408-6 and GIT 408-7,

locality 85-042; GIT 408-24, GIT 408-38–GIT 408-42, scales, and a shield fragment GIT 408-50, locality 85-042; Tabuska (Vishnevaya Gora) section, right bank of the Ufa River, downstream from the mouth of the Tabuska River, Ufa Amphitheatre, the Central Urals; Serga Subzone; Tabuska Beds, upper Ludlow (Modzalevskaya &

Märss 1991) or lower Pridoli (Shujskij 1981; Shurygina et al. 1981).

Occurrence. Lower Ludlow, glacial erratics of North Germany and Poland; Upper Ludlow of the East Baltic; upper Ludlow or lower Pridoli of the Central Urals.

Diagnosis. Relatively small cyathaspidid with dorsal shield 41 mm long and 25 mm wide and ventral shield up to 45 mm long and 26 mm wide; posterior margin transverse and weakly scalloped; lateral epitega narrow and short, not reaching the posterior end of central epitegum; anterior margin of ventral shield protruding anteriorly along mid-line. Dentine ridges on rostral epitegum (as far as seen) of short segments, on central epitegum medium to long and gently meandering, in places with double-ridge appearance; ridges relatively short laterally on postrostral field; higher and somewhat wider ridges intermittently with a number (1–4) of lower and narrower ridges; some higher ridges seemingly cross over lower ridges; on lateral epitega ridge distribution elliptical, long and of same width and height; density 4–6 ridges per mm; well-developed lateral line canal network (often of paired pores). [Diagnosis compiled after Kunth (1872), based on the shape of dorsal and ventral shields and supplemented by the dentine ridge pattern figured by Stensiö (1958, fig. 173A, B), and Figs 5, 6A–E herein].

Description. Specimen GIT 721-1 from Estonia represents a large patch of the dorsal shield (Fig. 2H). Its lateral line canal pattern (Fig. 6A) confirms that the fragment represents the central and part of both lateral epitega. The ridge pattern is similar to that seen on the photograph of a cast by Stensiö (1958, fig. 173A, B). The maximum length of our fragment is 3.1 cm, maximum width 2.2 cm. The sculpture is formed of gently meandering dentine ridges with the density of 4 ridges per mm. In some places, for example near the anterior end of the fragment, there are only 3 ridges per mm, perhaps due to the flattening of the whole fragment. The dentine ridges are of rather variable width if a narrow ridge is wedging in the pattern. Then the adjacent ridges become somewhat wider but the average density remains the same (4 per mm). In places, narrow and short ridges are wedged in between the long ones; some ridges can converge but then again become divided on the way backwards, and embrace new ridges. On the left side, the fragment shows double-ridges with two slightly higher ridges, while a very narrow lower ridge occurs between such double-ridge sets. Many ridges are long (up to 3 cm), extending from the anterior margin up to the posterior one. The dentine ridges are round-topped, situated rather close to each other; the margins of the ridges are smooth. Pores of the lateral dorsal

canal, medial dorsal canal and dorsal transverse commissures have been recognized on the specimen (Fig. 6A). The lateral line is often marked by specific ridges, entirely or partly embracing the pores (Fig. 2H). They are short and curvy, often ‘bone-like’ along the longitudinal lateral line canals, and some short ridges are even situated transversely. The ridges holding dorsal transverse commissure pores are slightly wider than the others.

Specimens of both the dorsal and ventral shields as well as the squamation are present in the Tabuska (Vishnevaya Gora) section. They show meandering ridges of varying width, which fit to the diagnosis by Denison (1964, p. 363), ‘a few of the ridges stand slightly higher than the others’.

Specimens GIT 408-3 and GIT 408-6–GIT 408-8 are broken pieces of dorsal shields (Fig. 5A–C, G). Specimen GIT 408-3 (Fig. 5A) is a fragment with all margins broken. It is 5 mm long and 5.5 mm wide, exhibiting 6 ridges per mm. Such a complicated pattern as seen herein may come from the dorsal shield, and if this is the case, from the right anterior part with the patch of curved ridges pointing to the pineal area; the shield is thinner and arched at this margin. The smoothly round-topped curvy ridges with fine side ridgelets are conspicuous. The double-pores in the lateral line canal (Fig. 6B) are a part of the right supraorbital canal.

Specimen GIT 408-7 is another fragment from the anterior part of the dorsal shield, part of rostral and central (+ lateral?) epitega (Fig. 5B). It is about 11 mm long and about 9.5 mm wide. The density of ridges is 6 per mm in the middle and the left side of the fragment. The dentine ridge pattern, which is complicated, and the lateral line pores have been used to define the orientation of the fragment (Figs 5B, 6C). The anterior margin of the shield (rostral epitegum) carries crosswise uniform ridges with a gently rounded surface. The relatively large area in about the middle of the fragment has both short and long curved ridges forming an oval pattern, with shorter curved ridges in the centre of that area and longer curved ridges around it (Fig. 5B). On the right side of the fragment, lateral to the lateral line canal, some ridges become anteriorly surrounded by a semicircular ridge while posteriorly they are rather straight and slightly narrower. Such a pattern is seen also on the left side, behind the crack. The lateral line is composed of eight distinct pores (Fig. 6C) occurring one after another in a line and not pairwise as in GIT 408-2 and GIT 408-3. The pores are supposed to belong to the right supraorbital canal.

Specimen GIT 408-6 is a rather big fragment (maximum length 15 mm, width 8.5 mm) of the middle and right part of the dorsal shield (Fig. 5C). It is identified as the dorsal shield because the ridge pattern is more complicated than that on the ventral side

(compare Fig. 5D). This fragment is distinctive due to its double-ridged sculpture occupying the main area of the fragment with none or one, seldom two narrow, short, low ridges occurring between the slightly higher double-ridge sets. In the anterior half (upper in the image) the curved or meandering ridges occur as relatively short segments, while posteriorly they become longer and are mainly straight. Meandering ridges can extend sideways over the narrower adjacent ridges. The ridges have a convex surface with 5–6 ridges per mm. The lateral line pores in this fragment (Fig. 6D) are placed in one not very distinct longitudinal row, the right medial dorsal canal and the dorsal transverse commissures are in three transverse short bits; three pores anteriorly might belong to the supraorbital canal. The pores form a ring-shaped pattern like that on the dorsal side in *Tolypelepis* (Märss 1977b, fig. 11A, B). Dentine ridges are densely packed; therefore, no ridgelets are seen on their margins.

Specimen GIT 408-8 (Fig. 5G) is a small, triangular fragment, 9 mm long along the left margin and 6 mm across the widest part. In its rather high and convex ridges, the fragment is similar to GIT 408-6 and is thought to originate from the dorsal shield; double-ridges are not present. Ridges are of medium width, 5.5–6 per mm. Up to four lower ridges are found between the stronger ones; although the prominent ridges have strongly rounded crests, the lower ones are rather flat. The fragment has four pores of the lateral line canal in a line, whereas two pores are situated in the angles where prominent ridges meet. The ridge margins have very fine crenulation or ridgelets, which are more regular on the dorsal shield than those on the scales (Fig. 3H, I for *Archegonaspis* sp., respectively).

Three specimens, GIT 408-2, GIT 408-4 and GIT 408-5 (Fig. 5D–F), have been identified as originating from the ventral shield. Specimen GIT 408-2 (Fig. 5D) is the left anterior half of the ventral shield. It is 1.7 cm long and 0.8 cm wide. There are 5–6 ridges per mm close to the broken edge and in the middle of the fragment and 7 in front of the shield; the vertically turned anterior margin carries 6 ridges per half a millimetre. The shield surface is anteriorly covered by beautifully curved ridges forming three sets. Ridges of one set are directed to the anterior margin, those of the other set turn back and then to the antero-ventral corner and ridges of the third set turn backwards of the shield. Lateral ridges join with those coming from the anterior part. Posteriorly the ridges are rather straight and longitudinal, whereas two to three relatively narrow lower ridges are situated between two higher and wider ones. Towards the shield margin the ridges are of uniform width and round-topped. A narrow band of fine tubercles of the same height and width (6 per mm) occurs at

the left unbroken shield margin. The ridges, which are placed more centrally on the shield, also show division into somewhat shorter lengths. The ventral lateral line system is represented by six pores of the post-oral canal, four pores possibly of the lateral ventral canal and two pores of the medial ventral transverse commissure (Fig. 6E).

Two fragments, GIT 408-4 and GIT 408-5, have a very similar sculpture. Specimen GIT 408-4 (Fig. 5E), with a concave lower surface, is 6.2 mm long and 7.5 mm wide and has 6–7 ridges per mm. Higher and wider long continuous ridges alternate with one or two narrower and shorter ones situated at a slightly lower level and close to each other. Some side-by-side higher ridges form double-ridges (Fig. 5E). All the ridges have meandering appearance; very fine ridgelets are seen on the sides of lower ridges. This fragment shows three lateral line canal pores. Fragment GIT 408-5 (Fig. 5F) is larger, 14.9 mm long and 14 mm wide and with just slightly coarser ridges (5–6 ridges per mm). The sculpture of the fragment is as in the previously described fragment GIT 408-4. Four longitudinally placed pores of lateral line canals emerge on the right side of the fragment. The origin of plates, dorsal or ventral, is difficult to specify, but based on the sculpture similarities with GIT 408-2, they are most possibly ventral. The worn surface (Fig. 5F) might also point to this being a ventral shield.

Scales GIT 408-38–GIT 408-41 represent dorso-lateral scales (Fig. 5H–K) and GIT 408-42 is a ventro-lateral scale (Fig. 5L). Anterior scales are high/wide but become smaller posteriorly. Anteriorly on the scales, behind the overlapped area, there occur transverse ridges, which posteriorly are replaced by teardrop-shaped or triangular tubercles. The main sculpture consists of alternating high and low dentine ridges similar to the shield dentine ridge pattern.

Archegonaspis bashkirica sp. nov.

Figure 7

- 1938 *Cyathaspis* sp. ind. Obruchev, pp. 36–38, pl. 1, fig. 1.
1938 *Cyathaspis*? sp. Obruchev, p. 38, pl. 1, figs 2, 3.

Etymology. After Bashkiria, the historical name for the Republic of Bashkortostan, Russia, where the specimens were found.

Holotype. The imprint of the external surface of the undivided dorsal and ventral shields No. 4650-1 (Obruchev 1938, pl. 1, fig. 1; Fig. 7B, C, herein; the original label in Fig. 7A with holotype data), housed in the Central Scientific Research Geological Museum, St Petersburg.

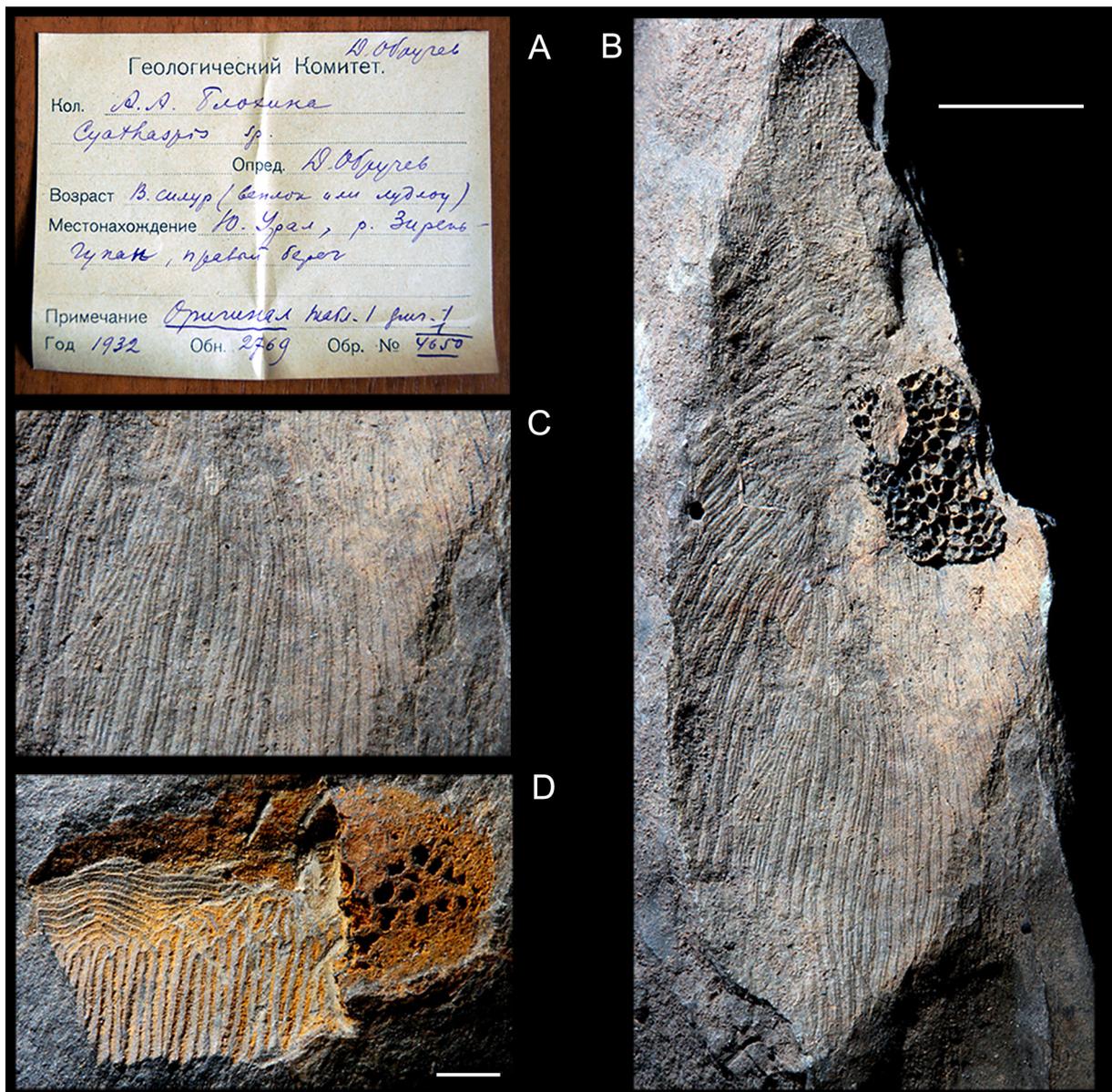


Fig. 7. *Archegonaspid bashkirica* sp. nov. **A**, original label of the holotype, the Central Scientific Research Geological Museum, St Petersburg; **B**, holotype No. 4650-1 (Obruchev 1938, pl. 1, fig. 1), the mould of the external surface of the undivided dorsal and ventral shields in the Central Scientific Research Geological Museum, St Petersburg; locality 2769, near the village of Irgizla, 15 km upstream of the mouth of the Siren-gupan River, right bank of this river, Belaya River basin, the Southern Urals, Bashkiria, Russia; age determined as Ludlow (Obruchev 1938, pp. 37–38); **C**, the close-up of the holotype in Fig. 7B; **D**, scale 4650-2 (Obruchev 1938, p. 38, pl. 1, fig. 2), locality 1944 of the same area as for holotype. Scale bars = 5 mm (B); 1 mm (D).

Paratypes. No. 4650-2 and No. 4650-3 (Obruchev 1938, pl. 1, figs 2, 3); paratypes come from locality 1944 of the same area as the holotype; the Central Scientific Research Geological Museum, St Petersburg.

Type locality and horizon. Locality 2769, near the village of Irgizla, 15 km upstream of the mouth of the Siren-gupan River, right bank of this river, Belaya River

basin, Southern Urals, Bashkiria, Russia; age determined as Ludlow (Obruchev 1938, pp. 37, 38).

Material. Holotype and paratypes.

Diagnosis. Sculpture pattern of invariably long dentine ridges of two widths, three narrower placed between two relatively coarser/wider ridges forming the sets (1:3:1);

ridge sets begin behind the tuberculated area anteriorly of the fragment and continue posteriorly as straight, nearly parallel longitudinal striped bands; ridge density 7–8 per mm behind tuberculated area.

Description. Specimen 4650-1 is a rather big (35 mm × 14 mm) mould of an undetermined fragment, where the sculpture is partly composed of sculptures of both the dorsal and ventral shields (Obruchev 1938, p. 37, pl. 1, fig. 1; Fig. 7B, C herein). The anterior about 1/5 of the shield is covered with small denticles or tubercles followed by a small number of short radiating ridges situated behind the tuberculated area (uppermost part in the figure); the transition from tubercles into ridges is not clear. Most of the specimen is occupied by long dentine ridges of two widths, with three narrower ridges placed between the two relatively coarse ones; the sets of ridges begin at the anterior part of the fragment and continue posteriorly as nearly parallel longitudinal striations. Such a sculpture persists on the fragment except for a strip with an arch-like distribution of the ridges running diagonally from the vacuoles down to the left corner in the figure (Fig. 7B, C), which seems like the course of a sensory line with most of the ornament passing across it.

The ridges are very fine. Two sets of ridges cover 1 mm of the posterior part of the specimen, meaning that there are about 8 ridges per mm measured in the figure, and about 7–8 ridges per mm behind the tuberculate area.

Two better-preserved scales are available. A pattern on the surface of the bigger but broken scale (7 mm × 4 mm) (4650-2; Obruchev 1938, p. 38, pl. 1, fig. 2; Fig. 7D herein) is composed of eight fine ridges parallel to the anterior margin and a set of longitudinally

and posteriorly directed ridges with 6–8 ridges per mm. Another scale in the collection (4650-3; Obruchev 1938, pl. 1, fig. 3) has ridges that diverge from the midline and are directed to two opposite directions.

Comparison

Four species of the genus *Archegonaspis* are compared, while the data on *A. schmidtii* (= *A. bimarica* Novitskaya specimen) are given for justification of its inclusion in *A. schmidtii* (Table 1).

Shield size. The dorsal and ventral shields of *A. lindstroemi* are very similar in length. The dorsal shield is 47 mm and ventral shield 44 mm long, with the difference of just 3–4 mm. The dorsal shield of *A. integra*, which seems to be broken posteriorly, is 41 mm and the ventral shield 45 mm long. *Archegonaspis lindstroemi* is the largest and *A. schmidtii* is the smallest species known from intact specimens (see measurements in Table 1). Geinitz (1884) kept two taxa, now called *A. schmidtii* and *A. integra*, very closely related because of their rather similar length : width ratios of the dorsal shield (42 : 23 mm and 41 : 25 mm, respectively). The East Baltic *A. integra* (specimen GIT 721-1) is perhaps the biggest as only the exposed central epitegum and partial lateral epitega are 22 mm wide, while the maximum width of *A. integra* from Geschiebe together with complete lateral epitega is 26 mm.

Shield margins. The shields are elongate oval in *A. schmidtii* and *A. integra* while in *A. lindstroemi* the shield is slightly more constricted anterior to the orbits. The anterior margin of the dorsal shield of *A. schmidtii* is distinctly convex. In *A. lindstroemi* the dorsal shield

Table 1. Comparison of some data on four *Archegonaspis* species. The ridge features were chosen from the central epitegum behind the rostral field. Measurement and sculpture data are from Geinitz (1884), Kunth (1872), Lindström (1895), Denison (1964) and Novitskaya (1970, table 1, p. 112) complemented herein. Dorsal or ventral shields of *A. bashkirica* are not defined. Ventral measurements of *A. lindstroemi* and *A. integra* are underlined

Taxon	Length (mm)	Width (mm)	Ridge density (per mm)	Ridge features
<i>A. schmidtii</i>	42	23	4–5 (6 on lateral epitegum)	Medium to long, slightly undulating, uniform width, ridge surface convex
<i>A. schmidtii</i> (= <i>A. bimarica</i>)	44	26	4–6	High and low on primordial zone, otherwise uniform width, medium to long, slightly undulating, ridge surface convex
<i>A. lindstroemi</i>	47 <u>44</u>	30 <u>29</u>	4–5	Long, uniform width, rather straight, ridge surface convex to flat, tessera-like units at posterior shield margin
<i>A. integra</i>	41(?incomplete) <u>45</u>	25 <u>26</u>	4–6	High and low, medium to long, meandering, ridge surface convex
<i>A. bashkirica</i>	35 incomplete	14 incomplete	About 7–8, on scale 6–8	High and low, long, straight

margin is anteriorly and posteriorly nearly transverse, while the posterior margin has a short median process; the anterior ventral shield margin is even slightly concave. In *A. integra*, as given in Kunth (1872), the dorsal shield narrows anteriorly but is partly broken posteriorly. There is an inconsistency in the orientation of the ventral shield in the illustrations of Kunth (1872, pl. 1, figs 3 and 6; discussion on p. 4) as, in the reconstruction (ibid., pl. 1, fig 3), this shield lies upside down if compared with the drawing of the specimen on the rock (ibid., pl. 1, fig. 6). The ventral shield narrows anteriorly from the anterolateral corners, forming an anterior transverse edge. Such an outline is very distinct for the *A. integra* specimen from the Central Urals (Fig. 5D), which implies that the reconstructed ventral shield of Kunth (1872, pl. 1, fig. 3) is correct.

Incomplete branchial plates are known in *Archegonaspis* species from Gotland Island (Heintz 1933, fig. 3), North Germany Geschiebe (Kunth 1872, pl. 1, fig. 6), Pioneer Island (Fig. 2F) and the Central Urals (Fig. 3F, G). A similarity between these plates lies in the elongate shape and uniform long dentine ridges (except the plate from Geschiebe whose sculpture is not known). The branchial plate in Fig. 3G is covered with ridges wedging off at the sharp edge (lateral angulation by Denison 1964) posterior to the branchial opening. The branchial opening is bordered by a notch seen in *A. lindstroemi* from Gotland and from the Geschiebe material (Heintz 1933), and from the Central Urals herein (Fig. 3G).

Overall sculpture. The sculptures of the shield surfaces of the *Archegonaspis* species treated here are similar in that the rostral epitegum (except *A. lindstroemi*, whose ridges are divided into short lengths) has a transverse dentine ridge pattern and the central and lateral epitega have a longitudinal dentine ridge pattern, although in all epitega there are specific variations. The overall density of ridges per mm on the shield remains between 4 and 6, except *A. bashkirica*, which has 7–8 ridges per mm.

Specific ridge pattern. The main differences at the species level lie in the details of dentine ridges and the patterns formed by ridges. Dorsal and ventral shields cannot be distinguished in *A. bashkirica* sp. nov. Sets of very long and straight ridges with wider (stronger) and narrower ridges alternate (1:3:1) on its shields except anteriorly on one shield bearing tubercles. *Archegonaspis schmidtii* and *A. integra* have ridges placed more elliptically than in *A. lindstroemi*. *Archegonaspis lindstroemi* has uniform long ridges of the same width on the central (except in the postrostral field and at the posterior margin) and lateral epitega of the dorsal shield and on the ventral shield (except in the anterior triangular area), whereas the ridge surface is rather smooth. The post-

rostral field is distinct in *A. lindstroemi* and less distinct in the *A. schmidtii* holotype, while in *A. integra* just half of it is preserved and it is therefore left out of the comparison. The specimens of *A. lindstroemi* have a few longitudinal tessera-like units posteriorly on the dorsal shield, while one unit forms a short median ridge that is lacking in *A. integra* and *A. schmidtii* (= *A. bimarisi* specimen; in the holotype that part of the shield is broken). Both *A. schmidtii* and *A. integra* have ridges of medium length on the central epitegum; however, *A. integra* shows a rather strong undulation and alternation of higher and lower ridges; the latter is lacking in *A. schmidtii*. In *A. schmidtii* (incl. the *A. bimarisi* specimen) and *A. lindstroemi* the length of ridges on lateral epitega may be nearly equal to the length of the epitega. A complicated arch-like distribution of continuous ridges is seen anteriorly on the ventral shield of *A. integra*, while *A. lindstroemi* displays there a simpler fan-shaped pattern of short ridge segments.

A few intraspecific variations in dentine ridge features of *A. integra* from three locations (East Baltic, the North Germany Geschiebe as published and the Central Urals) can be mentioned. The central epitegum of the dorsal shield of *A. integra* has wavy or meandering low and high ridges, which in spots may take a double-ridge appearance on *A. integra* from the Central Urals and Estonia. The Estonian *A. integra* specimen has longer and wider (4 per mm) ridges than *A. integra* from Geschiebe (5–6 per mm after Novitskaya 1970, p. 112).

Ridge surface. The ridge surface of *A. lindstroemi* is mostly flat, which is especially well exhibited on the SEM images (Fredholm 1988, fig. 3A–C). The other species have mainly convex ridge surfaces, or angular surfaces on the ridges from marginal areas of the shields.

Lateral line sensory system. In Märss (1977a, fig. 3A–C) the continuous lines in the *Archegonaspis* head shield were shown as a supposed course of supraorbital canals. The new material was not suitable for using anise oil to make the segments between the pores transparent to see whether the canals were continuous or not. The lateral line system is well developed and pores distinct in *A. integra* from Estonia (GIT 721-1, Fig. 6A) and the Central Urals (Fig. 6B–E). Small pores of the supraorbital canal are also detected in the rostral epitegum and the anterior part of the central epitegum of *A. schmidtii* and *A. lindstroemi* (Märss 1977a, fig. 3A, C, respectively). In Estonian specimens the pores are very distinct, being somewhat deeper and larger than those in the Central Urals. Two very fine pores of the lateral line canal occur near the anterior margin at the midline of the branchial plate in *A. ?lindstroemi*, where they possibly form a branchial transverse commissure connecting the dorsal

and ventral lateral line systems. Prior to this finding, pores near the anterior ends of the branchial plates were known in *Poraspis* and *Anglaspis* (Denison 1964, p. 330).

Anomalous shields. Patches of various size and somewhat atypical dentine ridge distribution have been established on the shields of several cyathaspidid taxa, which are interpreted either as normal growth products or growth anomalies (Denison 1964, p. 462; Dineley & Loeffler 1976, pp. 104–107; Elliott & Petriello 2011, pp. 523–524). An anomalous patch is evident at the posterior end on the shield of *Archegonaspis lindstroemi* (Fig. 3E), demarcated by the discontinuity of ridge distribution. This indicates some abnormalities in the growth of that particular shield, the cause of which is not clear. Most possibly the patch is a fractured and healed area of that shield. A specimen with a patch of ridges, called the primordial zone, was described by Novitskaya as a new taxon *Archegonaspis bimariss* (1970, pp. 112–113, pl. 9, figs 1, 2). The margins of that patch are clearly delineated from the rest of the dorsal shield and it seems more like an aberrant growth of that shield than a specific characteristic of a new taxon. The morphology and the sculpture of this shield resemble those of *A. schmidti* (see more discussion below).

Subfamily CYATHASPIDINAE Kiaer, 1932

Type genus. *Cyathaspis* Lankester, 1865.

Remark. Kiaer (1932) included in his new family Cyathaspididae three genera: *Cyathaspis* Lankester, 1856, *Archegonaspis* Jaekel, 1927 and *Eoarchegonaspis* Kiaer, 1932. *Eoarchegonaspis* was synonymized by Denison (1964, p. 367) under *Vernonaspis* Flower & Wayland-Smith, 1952. The genus *Cyathaspis* was treated by Kiaer (1932) and is also treated herein under the subfamily Cyathaspidinae Kiaer, while *Archegonaspis* Jaekel has been removed here to Archegonaspidinae subfam. nov.

Diagnosis. Dorsal shield wide, anteriorly strongly narrowing; epitega distinct; dentine ridges of medium length, shorter than in Archegonaspidinae subfam. nov. and longer than in Tolypelepidinae Denison, 1964; ridges form tessera-like units of different distinctness; postero-median crest dorsally and ventrally long; lateral longitudinal ridge bands of ventral shield wide.

Genus *Cyathaspis* Lankester, 1865

Type species. *Pteraspis banksi* Huxley & Salter, 1856.

Species content. *Cyathaspis banksi* (Huxley & Salter, 1856); *Cyathaspis acadica* (Matthew, 1886); *Cyathaspis alexanderi* sp. nov.

Remarks. On the basis of the sculpture pattern, *Cyathaspis* sp. ind. and *Cyathaspis*? sp. from the Belaya River Basin, Southern Urals, Russia (Obruchev 1938) are excluded from the genus *Cyathaspis* and placed within the genus *Archegonaspis*.

Diagnosis. Epitega of dorsal shield distinct; the post-rostral field may also be distinct; ridges of medium length form narrow tessera-like units on central epitegum; medial ridge prominent and gently wavy, flanking ridges lower and narrower; long uniformly shaped ridges on lateral epitega; ridge density 5–8 per mm; ventral shield with wide lateral bands of long and uniform ridges (Denison 1964, modified).

Occurrence. Shropshire and Herefordshire, Britain, Přidoli; New Brunswick, Canada, upper Silurian; the Central Urals, Russia, Upper Ludlow or lower Přidoli, upper Silurian.

Cyathaspis alexanderi sp. nov.

Figure 8A–F, H

Etymology. After Dr Alexander Zhivkovich, a friend and one of the leaders of several expeditions to the Central Urals.

Holotype. GIT 408-14 (Fig. 8A), a large fragment of the right side of the ventral shield from locality 85-042.

Paratypes. GIT 408-15 from locality 85-146-5D; GIT 408-16, GIT 408-17, GIT 408-18 and GIT 408-19 from locality 85-042.

Type locality and horizon. The geographical and stratigraphical data of all specimens are the same: Tabuska (Vishnevaya Gora) section, right bank of the Ufa River, downstream from the mouth of the Tabuska River, Ufa Amphitheatre, the Central Urals; Serga Subzone; Tabuska Beds, upper Ludlow (Modzalevskaya & Märss 1991) or lower Přidoli (Shujskij 1981; Shurygina et al. 1981).

Diagnosis. Dorsal and ventral shield main area covered by weakly expressed tessera-like units having straight or gently meandering prominent medial ridge accompanied by 2–3 lower ridges on its flanks; prominent medial ridge in units 2–5 mm long; ridge density 6–7 per mm; endings and beginnings of prominent medial ridges do not follow one after another but slightly overlap each other. Ventral shield margin with wide band of ridges parallel to each other and to shield margin.

Description. The holotype GIT 408-14 (Fig. 8A) is a big fragment of the right side of the ventral shield. It is strongly convex, up to 12 mm long and 12 mm wide.

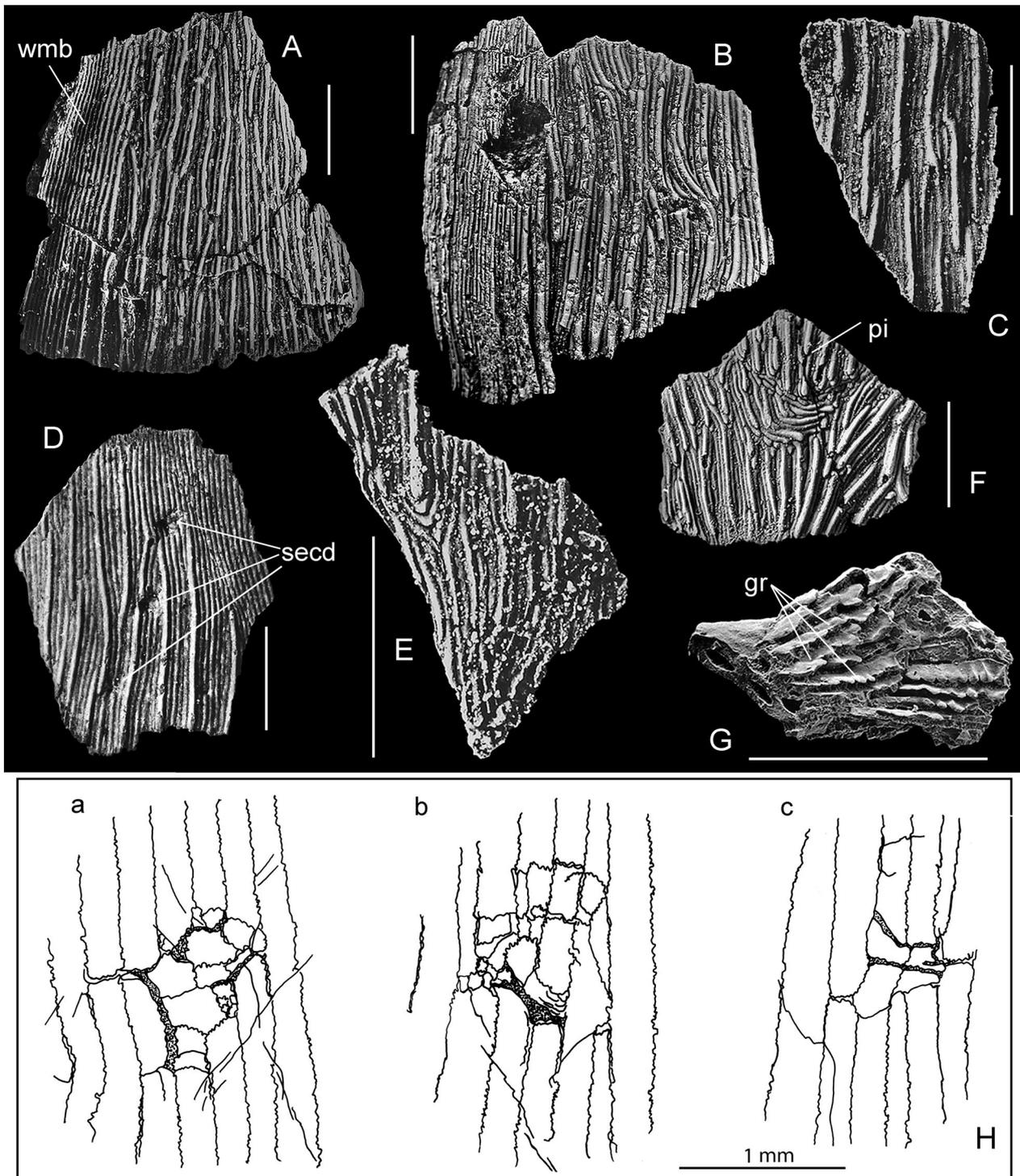


Fig. 8. *Cyathaspis alexanderi* sp. nov. **A–F:** A, holotype, a big fragment from the right side of the ventral shield, GIT 408-14; B, fragment possibly from the dorsal shield, GIT408-15; C, D, shield fragments of unknown position on the body, D, with healed bite marks, GIT 408-16 and GIT 408-17; E, small piece of possibly the dorsal shield, GIT 408-18; F, fragment from the midline of the dorsal shield, most possibly from the pineal area, GIT 408-19; **G,** *Cyathaspididae* gen. et sp. indet., the element of the possibly branchial region, GIT 408-20; **H,** bite marks in D (a, the anteriormost, followed by b and c) with small tubercles and a deeper groove on the bottom of each pit. Scale bars = 3 mm (A–F); 1 mm (G). *Locations:* A, C–G, locality 85-042; B, locality 85-146-5D, Tabuska (Vishnevaya Gora) section, the Central Urals, Tabuska Beds either of the lower Pridoli (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow level (Modzalevskaya & Märss 1991). *Abbreviations:* gr, possible gill rakers; pi, possibly pineal macula; secd, secondary denticles in the healed wounds; wmb, wide marginal band of uniform ridges.

The right margin, the 2.5 mm wide band, bears long and straight uniform-sized ridges. The density of ridges is 6–7 per mm on the right margin, 6 per mm on the mid-shield (main area). The sculpture pattern on the main area is of gently meandering segments of prominent medial ridges, alternating with 2 to 3 lower ridges, the medial one of which is in turn lying on the lowest level. The ridges arranged this way form long units, somewhat tessera-like structures, where the endings and beginnings of the highest ridges do not follow one another but slightly overlap each other. The length of prominent ridges is 2–5 mm. The sculpture of this specimen seems slightly worn. Three small pores of the lateral line run longitudinally along the main area close to the lateral band, and one pore is located medial to that line. The ridge margins have a longitudinal row of tiny ‘grains’, which cannot be called denticles or serrations. Two features show that the fragment definitely is a ventral shield: the marginal wide ridge band (see Denison 1964, fig. 111 for *C. acadica*) and the placement of pores of the lateral line system.

Specimen GIT 408-15 (Fig. 8B) is a fragment with a maximum length of 10.2 mm and width of 10 mm with the left intact margin arched antero-posteriorly. Its sculpture is rather deep and not worn as in the above-described specimen; therefore it might be from the dorsal shield. The ridges are long, very narrow (12 ridges per mm) and parallel to each other near the left margin but here also two wider ridges occur among narrower ones which are not observed in the ventral marginal band of GIT 408-14. The fragment is convex with the left margin turning down. The main area shows a rather regular alternation of three lower ridges between two higher ones, with the overall density of 5 ridges per mm on the right half of the fragment. Some ridge sets meander considerably, but the feature where the posterior ridge starts before the anterior one ends is clear and the tessera-like appearance of units is rather distinct (but less distinct than on the specimen in Fig. 8A). The length of prominent ridges is between 2.3 and 3.3 mm.

Specimen GIT 408-16 (Fig. 8C) is a small fragment of unknown location on the shield, 7.2 mm long and 3.8 mm wide, with all margins broken. The mostly parallel high (white in the picture) sharp-crested ridges alternate with 2–5 lower flat-crested ones, with a density of 6.5–7 ridges per mm. The 1.9–5.0 mm long, stronger ridges do not follow one another successively but their ends overlap each other.

Specimen GIT 408-17 (Fig. 8D) is of unclear origin. It is 9 mm long and 7 mm wide. A suture in the external ridge pattern divides the surface into the left side with stronger and gently curved ridges and the 1.2–1.5 mm wide right side with uniform, fine and gently curved ridges. Distinctly convex high ridges alternate with 3–6

lower ones; at the right anterior margin there are up to 9 fine (lower) ridges. The margins of ridges have very fine posteriorly rising oblique ridgelets. The visceral side has a longitudinal concavity and an overlapping area on the right anterior part below the finest sculpture. The fragment becomes thicker to the left of the suture. A single pore of the lateral line canal on the longitudinal midline, where a few ridges join, is surrounded by an oval wall.

Diagonally on the fragment there are three pits of nearly the same size and orientation (Fig. 8D), where the regular ridges are broken and pressed down. Distances between the pits are 2.4 and 2.5 mm. The bottom of each pit shows an elongate, slightly crescent-shaped deeper groove and short fine tubercles on one side of it (Fig. 8H: a–c). The tubercles are better expressed in two more anterior pits (Fig. 8H: a, b). Fine cracks run diagonally through the ridges close to the pits. These pits are interpreted as the biting imprints on this *Cyathaspis* shield, hinting at the attackers of these agnathans, for example, the eurypterids, which may have caused these wounds by their spiked claws (chela). These marks are externally similar to earlier described (Elliott & Petriello 2011, p. 526, fig. 7A, B) three puncture wounds on the dorsal shield of *Lechriaspis patula*, which were also formed by predation by an eurypterid.

Specimen GIT 408-18 (Fig. 8E) is a very small piece (as a maximum 5 mm long and 2.7 mm wide) possibly of a dorsal shield, which carries distinct (maybe too distinct for this taxon) elongate tessera-like units. Three ridges rise stepwise towards the prominent ridge embracing it posteriorly. Their anterior ends are broken and therefore it is not clear whether the ridges form a closed perimeter around the prominent medial ridge or not. There are 3–9 narrow ridges between the medial prominent one. The prominent ridges are round-crested and lower ridges sharp-crested.

Specimen GIT 408-19 (Fig. 8F), 6.5 mm long and 7.2 mm wide, comes from the midline of the dorsal shield, most possibly from the pineal area. The upper, external surface of the shield is convex and the lower, visceral surface is concave, with the deepest part located posteriorly beneath the medial longitudinal ridges. The shield sculpture appears on three levels. On the lowest level, the main shield carries rather long ridges with a prominent ridge and relatively many (up to 5) low ridges on its flanks. The next level has shorter ridges than the previous one. Here, about the midline, the ridges turn to the right at a right angle. The highest level is embraced by short ridgelets and tubercles; this ridge grouping has short prominent ridges, each surrounded by a number of low ridges. All ridges are round-crested and with oblique serration on the margins.

Cyathaspis ?alexanderi sp. nov.

Figure 9A–C

A few specimens (GIT 408-43, GIT 408-45 and GIT 408-46) (Fig. 9A–C) have small, tessera-like units externally. The units are built of closed, ring-like or paired ridges (Fig. 9A), in some units part of ridges are arranged semicircularly (Fig. 9B, C). The ridges are fine, 6–8 per mm, relatively high. Each more central ring or pair of ridges lies stepwise on the higher level, forming small towers. The highest number of such ridge pairs in a unit is six, plus the central ridge. One fragment has two pores of the lateral line system (enlarged in Fig. 9A). Due to the low number of such ornamented specimens and a specific high tower-like construction, they may have been situated close to the pineal macula as seen in *Cyathaspis acadica* (Denison 1964, fig. 111) and *Tolypelepis undulata* (e.g. Stensiö 1958, fig. 169A). The ridge pattern of the tessera-like units is somewhat similar to that of *Tolypelepis* whose main sculpture units are still larger and much more flattened and each tessera- or scale-like unit is of pairs of ridges on the sides, while in *C. ?alexanderi* the ridges may form closed rings, one

ring partly resting on the ring below; such sets may form rather high ‘towers’. Due to significant differences with *Tolypelepis*, our specimens may belong to *Cyathaspis* species, which are rather common in these two localities (85-042 and 85-146-5D).

Cyathaspididae gen. et spp. indet.

Figures 3J–M, 8G

The fragments (GIT 408-49, GIT 408-51, GIT 408-52, GIT 408-53), chosen for showing the fine denticles on the ridge margins (Fig. 3J–M), belong to taxa left in open nomenclature in the subfamily Cyathaspidinae. They are covered with curved ridges of different lengths or short denticles, all with prominent crenulation at their margins. One fragment has a pore of the lateral line system (Fig. 3L). The curved ridges somewhat resemble those in Fig. 9A–C.

A tiny fragment GIT 408-20 (Fig. 8G) has only the surface and one margin intact. The surface shows blades, about 7 on the narrower end and about 10 on the wider end of the fragment, which are equipped with triangular sawteeth-like structures. Most possibly the

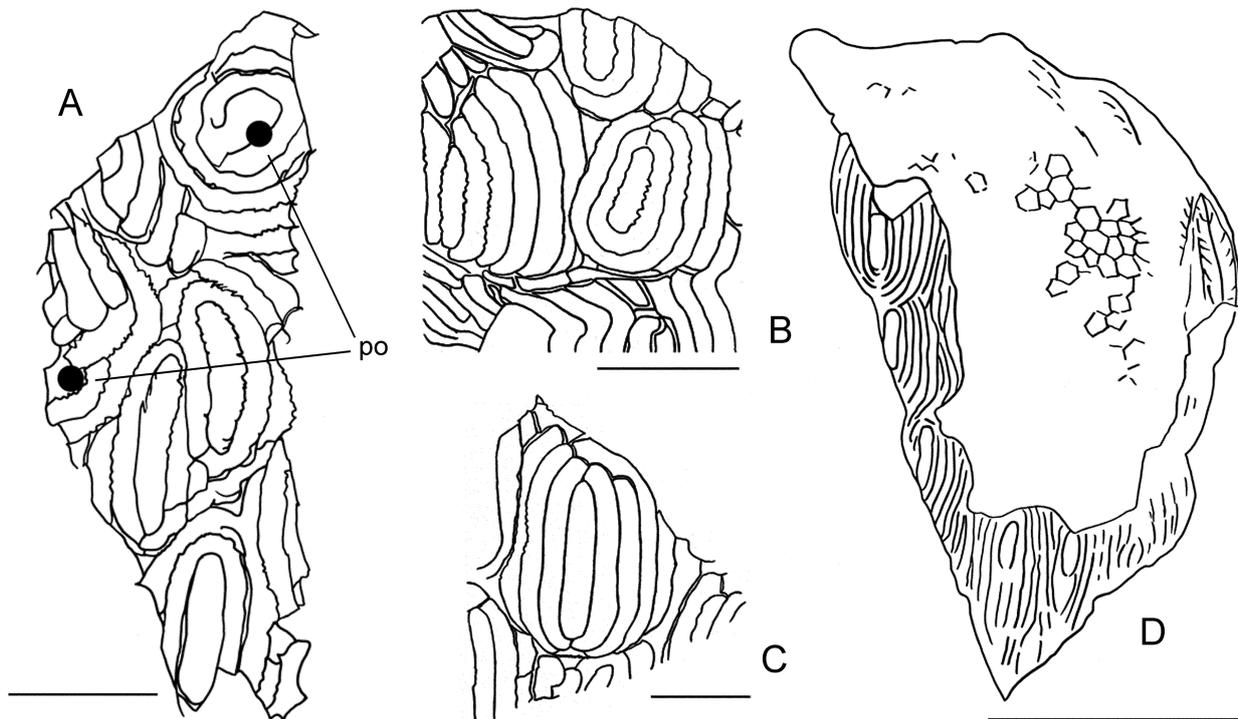


Fig. 9. A–C, *Cyathaspis ?alexanderi* sp. nov.: shield fragments: A, GIT 408-46; B, GIT 408-45; C, GIT 408-43; D, *Tolypelepis* sp. indet.: shield in visceral view, GIT 721-5. Scale bars = 1 mm (A–C); 5 mm (D). Locations: A, C, locality 85-042; B, locality 85-146-5D, Tabuska (Vishnevaya Gora) section, the Central Urals, Tabuska Beds either of the lower Pridoli level (Shujskij 1981; Shurygina et al. 1981) or upper Ludlow (Modzalevskaya & Märss 1991); D, locality 8825-11/15a, Right Anuchin River, Cape Vize, north of Northern Island, Novaya Zemlya Archipelago; uppermost part of the Konstantinovskaya Formation, Pridoli, upper Silurian. Abbreviation: po, pores of lateral line canals (pores shown larger than they are in reality).

specimen comes from the branchial region (with gill rakers?). The vacuoles of the cancellous layer of the plate are exhibited on the broken surfaces. Due to scanty features, the taxon which the piece belongs to is not known.

Comparison

Cyathaspis alexanderi sp. nov. has a few features preserved that can be compared with two other *Cyathaspis* species (data on *C. acadica* and *C. banksi* from Denison 1964; Table 2). The most certain feature is the grouping of ridges into tessera-like units which cover the central parts of the dorsal and ventral shields of all three species (*Cyathaspis alexanderi* sp. nov., *C. banksi* and *C. acadica*). The units are of medium size in *C. acadica* and *C. alexanderi* sp. nov.; they seem to be long in *C. banksi* (Denison 1964, fig. 110). The ridge density on the dorsal shield is 5 ridges per mm in *C. alexanderi* and *C. banksi* and 7–8 per mm in *C. acadica*. *Cyathaspis banksi* and *C. alexanderi* have wide lateral bands of parallel ridges on the ventral shield. The pores of lateral line canals are small but distinctive in *C. alexanderi* sp. nov., while the lateral line canal system is not known in *C. acadica* and *C. banksi*.

Subfamily TOLYPELEPIDINAE Denison, 1964

Type genus. *Tolypelepis* Pander, 1856.

Content. *Tolypelepis* Pander, 1856; *Asketaspis* Dineley & Loeffler, 1976; Tolypelepidinae gen. indet. herein. We agree with Janvier (1996) and exclude *Athenaegis* Soehn & Wilson, 1990 from the Tolypelepidinae on the basis of the features of the branchial region – *Athenaegis* has a branchial area of separate scales and longer platelets (Soehn & Wilson 1990, p. 407), while *Tolypelepis* has a single plate on both sides.

Diagnosis. Rostral epitegum of short ridges or denticles placed transversely; central epitegum composed of short

tessera-like or scale-like units or short longitudinal ridges; lateral epitega covered by discontinuous longitudinal ridges; ventral shield anteriorly occupied by tessera-like units entirely or partly simultaneously with longitudinal ridges of medium length; posterior zig-zag margins of both shields strongly convex; branchial plate with one to two longitudinal rows of tessera-like units; lateral line canals composed of closed short segments forming longitudinal and perpendicular line pattern (Denison 1964, updated).

Genus *Tolypelepis* Pander, 1856

Type species. *Tolypelepis undulatus* Pander, 1856.

Species content. *Tolypelepis undulata* Pander, 1856; *T. lenzi* Dineley & Loeffler, 1976; *T. leopoldensis* Loeffler & Jones, 1977; *Tolypelepis bedovensis* sp. nov.

Remarks. *Tolypelepis timanica* Kossovoy & Obruchev, 1962, has been in the lists as nomen nudum but recently was synonymized under *T. undulata* Pander by Novitskaya (2004) with an indicated distribution in the upper Silurian. *Tolypelepis mielnikensis* Dec (2015) is synonymized under *T. undulata* Pander herein (see Remarks for *T. undulata* below).

Diagnosis. Median rostral process absent; orbital notches shallow; rostral epitegum covered with transverse short ridges or denticles and central epitegum with tessera-like units anteriorly and scale-like units posteriorly; in each unit central ridge broader and higher than surrounding ones; postrostral field distinct; lateral epitega with discontinuous longitudinal ridges; ventral shield covered with tessera-like units anteriorly and posteriorly, while central part and relatively narrow lateral bands are of longitudinal ridges; branchial plate with one to two rows of tessera-like units along the plate; infraspecific sculpture variations occur (amended from Denison 1964; Märss 1977b; Soehn & Wilson 1995; Novitskaya 2004).

Table 2. Comparison of three *Cyathaspis* species. Explanations: ventral measurements are underlined; data for *Cyathaspis banksi* and *C. acadica* from Denison (1964)

Taxon	Length (mm)	Width (mm)	Ridges per mm	Ridge pattern
<i>C. alexanderi</i>	?	?	5 <u>6–7</u>	Ridge units of medium size, prominent ridges (1.9–5 mm long) separated by 3–5 finer ones
<i>C. banksi</i>	38–45	26–38	5	Long? ridge units: one coarse ridge separated by 1–5 finer ones
<i>C. acadica</i>	Smaller than <u><i>C. banksi</i></u>	Smaller than <u><i>C. banksi</i></u>	7–8	Ridge units of medium size

Occurrence. East Baltic (Estonia, Latvia, Lithuania) and East Poland; Timan-Pechora Region (North Timan), Novaya Zemlya and Severnaya Zemlya archipelagoes; Pridoli, upper Silurian; Mackenzie District, late Silurian or Early Devonian for *T. lenzi* (Dineley & Loeffler 1976); Somerset Island, Late Ludlow or Pridoli for *T. leopoldensis*, Northern Canada (Loeffler & Jones 1977).

Tolypelepis undulata Pander, 1856
Figures 6F, G, 10A–D

(for extended synonymy see Novitskaya 2004, pp. 103–104).

2015 *Tolypelepis mielnikensis* Dec; pp. 638–643; figs 3, 4.1, 4.2.

Remarks. *Tolypelepis undulata* was originally described by Pander (1856) from the Ohesaare Cliff, southern Saaremaa Island, Estonia, from the beds today known as the Ohesaare Stage, upper Pridoli, upper Silurian. Pander (*ibid.*, p. 61) treated under *Tolypelepis* only one species ('Nur eine Species' from 'Fundort Ohhesaar'). Another name, *Oniscolepis magnus*, was used by him for a scale (*ibid.*, pl. 6, fig. 32b), which later (Rohon 1893; Gross 1947, 1961; Märss 1977b) was assigned to *T. undulata*. Schmidt (1893) described the dorsal shield of this species under a new generic name *Tolypaspis undulata* and Rohon (1893, pp. 79–88) followed him using the same generic name. Kiaer (1932, pl. 10) distinguished Schmidt's specimen No. 257/592 as its genotype and holotype. Nevertheless, the generic name *Tolypaspis* Schmidt is a junior synonym of *Tolypelepis* Pander, and is not valid. The type material of Pander, the shield fragment, is lost but the type locality has continuously produced *T. undulata* specimens. It is the only cyathaspidid heterostracan found in the Ohesaare Cliff locality and has been re-described or treated or mentioned several times (e.g. Kiaer 1932; Stensiö 1958, 1964; Obruchev 1964; Märss 1977b; Novitskaya 2004; Dec 2015).

Dec (2015) described and established a new species *Tolypelepis mielnikensis* from a depth of 602.3–606.8 m in the Mielnik drill core, eastern Poland (Pridoli, upper Silurian), including in this taxon also a few specimens described earlier from Estonia under *T. undulata* (*ibid.*, figs 4.3 and 4.4). Dec (*ibid.*) considered *T. mielnikensis* unique due to its rostral region which is constricted at orbital level. The Mielnik specimens of *T. mielnikensis* Dec (2015) are poorly figured, therefore it is not possible to use this publication for comparison. A short study of the same Mielnik core specimens in Warsaw (remarks from the author's personal observations in 1984, 1988) did not show any major differences in the sculpture pattern. Also, the widening of shields might be the result

of the sedimentation and preservation peculiarities, which are often seen in other specimens; it is not a very reliable feature for making decisions about the taxon. Establishing a new species was in this case unreasonable, and thus this taxon is herein treated as a junior synonym of *T. undulata* Pander.

Neotype. Specimen No. 257/592, Central Scientific Research Geological Survey Museum, St Petersburg. As the type material of *Tolypelepis undulata* Pander, 1856 is not preserved, the holotype chosen by Kiaer (1932, pl. 10) is recognized here as having neotype status (ICZN 1999, Article 75.1).

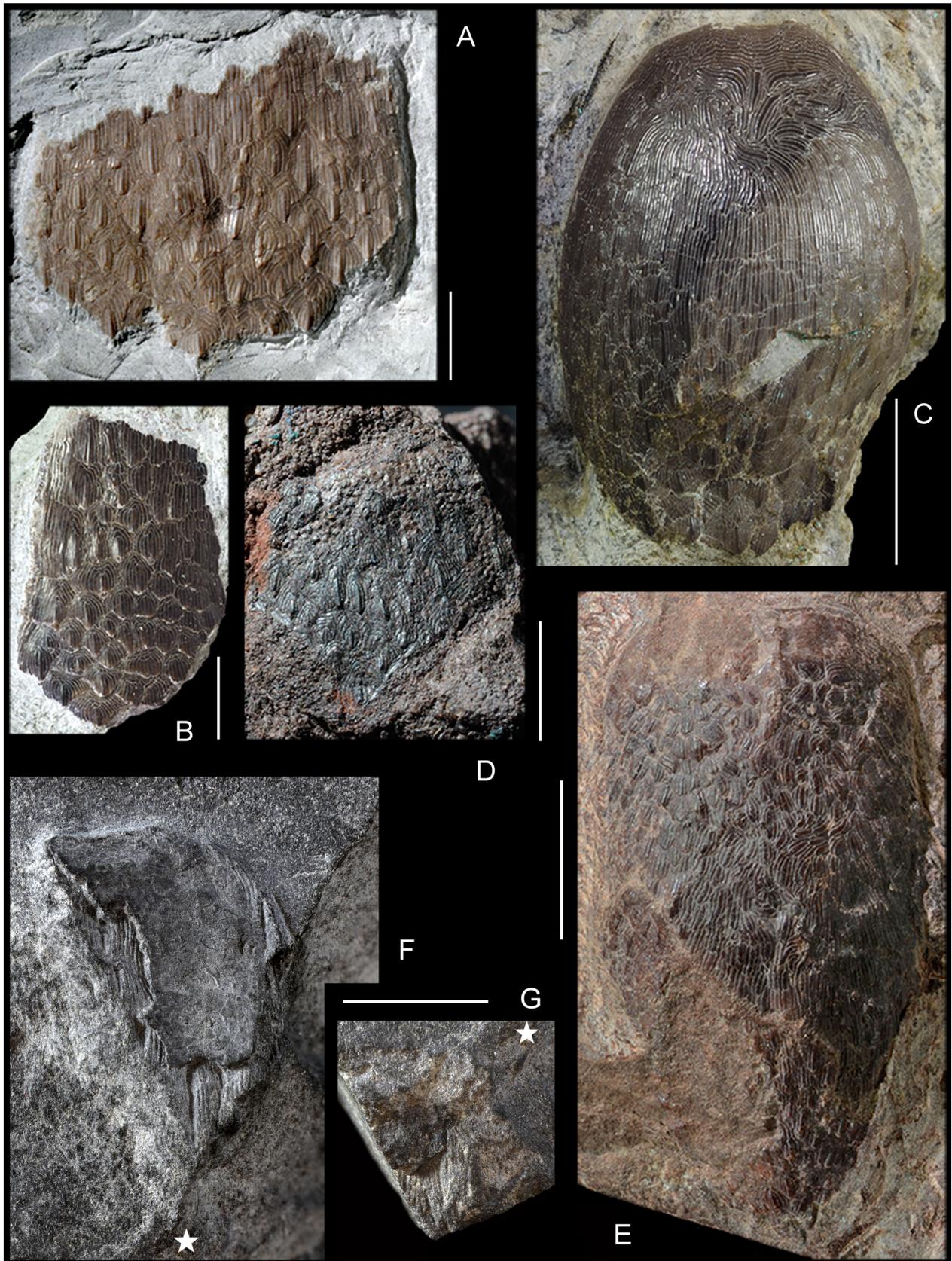
Type locality and horizon. Ohesaare Cliff, Saaremaa Island, Estonia; Ohesaare Stage, Pridoli, upper Silurian.

Material. Large dorsal and ventral shield fragments from the Ohesaare Cliff outcrop and from depths of 176.1 and 176.2 m, Ruhnu drill core, Estonia, Ohesaare Stage, upper Silurian; anterior part of the ventral shield of *T. undulata*, from a depth of 401.8 m, Butkunai drill core, Lithuania, upper Silurian (Märss 1977b); a large fragment of *T. undulata* dorsal shield (GIT 721-3) from a depth of 162.5 m, Kolka-54 drill core, Latvia; ventral shield and a dorsal shield fragment (respectively TUG 68-1 and TUG 1384-13) from the Ohesaare Cliff, Saaremaa, Estonia. *Tolypelepis undulata* dorsal? shield fragment (GIT 721-4) from a depth of 79.8 m, Velikaya River-81 drill core, North Timan, Greben' Stage, thelodont *Trimerolepis timanica* vertebrate zone, uppermost Pridoli, upper Silurian.

Occurrence. Pridoli of the East Baltic (Estonia, Latvia, Lithuania), Poland and North Timan.

Diagnosis. Length of dorsal shield 32–38 mm, width 25 mm; average dentine ridge density on dorsal shield 4 per mm (2 on central epitegum and 8 on lateral epitega); ventral shield 36 mm long; shield with rather narrow lateral bands; 3–4 ridges per mm on central part and 4–5 ridges per mm on lateral bands; sculpture ridge pattern either tessera-like or scale-like, or shield partly longitudinally ridged; two rows of tessera-like units longitudinally on branchial plate; dentine ridges rounded; sculpture units of medium size, 1.8(±0.3) mm long and 1(±0.2) mm wide (unit measurements from Dec 2015, p. 639).

Description. Two specimens found in recent decades represent partial dorsal shields. Specimen GIT 721-3 (Fig. 10A) is a flattened posterior half of the shield (20 mm long and 22 mm wide) with lateral margins turning down. The posterior margin is slightly broken between the scale-like units. The characteristic pore distribution of lateral line canals confirms that the speci-



men is the dorsal shield (Fig. 6G). A small fragment TUG 1384-13 (Fig. 10B) (20 mm long and 13 mm wide) is the left postero-lateral corner of the dorsal shield. It has the posterior end of the lateral epitegum with the overlapping margin on the left side where six wider and two finer long or discontinuous ridges cover this area. The left posterior margin of the shield is rather straight when unbroken. In both specimens the sculpture units are tessera-like more anteriorly of the fragment and scale-like more posteriorly, where they slightly overlap the unit behind. In both specimens the median higher ridge is embraced by the obliquely placed short ridges or denticles anteriorly and 3–5 longitudinal elongate ridges on both sides; the highest number of side ridges is 9 per one side in TUG 1384-13. As a rule, the numbers of side ridges increase towards the posterior ends of the units. The scale-like units have the median ridge rising posteriorly and accompanied anteriorly and laterally by a rather high number of ridges. Some scale-like units go beyond the posterior margin, giving it a zig-zag outline.

The almost complete ventral shield TUG 68-1 (Fig. 10C) is oval in outline, as a maximum 32 mm long and 22 mm wide. The shield is strongly convex in cross section, the anterior and lateral margins are smoothly arched, the posterior margin has zig-zag appearance due to scale-like units. The anterior and lateral margins are covered with parallel ridge bands, while anteriorly they lie transversely and on the sides curve according to the margin of the shield. The area behind the anterior transverse parallel ridge band has ridges distributed in a fan-like manner, with a number of higher ones in between. The central area of this ventral shield consists of groups with a relatively long median ridge and one to two shorter ridges laterally. The well-expressed tessera-like units lie between this area and the parallel lateral ridge bands. The posterior about one-third of the shield is covered with units in which the median ridge is higher, and slightly wider than the surrounding ridges anteriorly and laterally. Specifically these units slightly cover the units behind, making them scale-like. The lateral line system is well developed and of cyathaspidid character (Fig. 6F), with post-oral and lateral and medial

ventral canals and lateral and medial ventral transverse commissures.

Specimen GIT 721-4, 11 mm long and 12 mm wide, is given as an example of the sculpture of the same taxon from the North Timan (Fig. 10D). All specimens, even very broken, display similar tessera-like or scale-like units. This particular specimen, possibly of the dorsal shield, shows up to seven oblique ridges anteriorly, embracing the mid-ridge. There is a weak subdivision of oblique ridges into denticles.

Tolypelepis bedovensis sp. nov.

Figures 6H, 10E

Etymology. From the name of the River Bedovaya, where the specimen was found.

Holotype. GIT 721-7, the ventral shield, broken postero-laterally and posteriorly.

Type locality and horizon. The Bedovaya River section, October Revolution Island, Severnaya Zemlya Archipelago; very hard red limestone beds of the Krasnaya Bukhta Formation, the lower part of the formation, upper Silurian (unpublished data of Khapilin & Markovskij in Matukhin et al. 1999, pp. 3, 33).

Material. Only the holotype is known.

Diagnosis. Small *Tolypelepis* with 37 mm long (incomplete) and 20 mm wide elongate oval ventral shield; the main surface covered with short and relatively uniform tessera-like units 1.4–2.3 mm in length and 0.9–1.5 mm in width; units become slightly longer and scale-like posteriorwards and slightly overlap the posterior units; each unit has transverse ridges anteriorly, wide medial and 1–4 flanking ridges, often unsymmetrically placed on sides; ridges relatively coarse, 4 ridges per mm; ridges higher anteriorly and posteriorly but lower and more simple at mid-part of the ventral shield; anterior and lateral marginal dentine ridge band about 3 mm wide and covered with fine parallel ridges, 8 ridges per mm.

Fig. 10. *Tolypelepis* species, shields and shield fragments. **A–D**, *Tolypelepis undulata* Pander; **E**, *Tolypelepis bedovensis* sp. nov.; **F, G**, *Tolypelepis* sp. indet. **A**, posterior part of the dorsal shield, GIT 721-3; **B**, left postero-lateral part of the lateral epitegum of the dorsal shield, TUG 1384-13; **C**, almost complete ventral shield, TUG 68-1; **D**, sculpture on GIT 721-4; **E**, ventral shield with the posterior left side broken, GIT 721-7; **F**, shield in visceral view; **G**, small piece of shield from the most posterior part of (F), GIT 721-5 [to save the space of the figure, the lower part of (F) was cut off (=G); white stars indicate the points to assemble the two pictures]. Scale bars = 5 mm (A, B, D, F); 1 cm (C, E). *Locations:* A, Kolka-54 core, depth 162.5 m, Latvia; B, C, Ohesaare Cliff, Saaremaa Island, Estonia; D, Velikaya River-81 core, depth 79.8 m, North Timan; E, Bedovaya River section, October Revolution Island, Severnaya Zemlya Archipelago, lower part of the Krasnaya Bukhta Formation, upper Silurian (data of Khapilin & Markovskij in Matukhin et al. 1999, pp. 3 and 33); F, locality 8825-11/15a, Right Anuchin River, Cape Vize, north of Northern Island, Novaya Zemlya Archipelago; uppermost part of the Konstantin Formation, Pridoli, upper Silurian.

Description. The specimen was mostly hidden in the rock and was mechanically cleaned with a needle. As a result, the ventral shield (Fig. 10E) is mostly disclosed, and the most characteristic features are available for diagnosis allowing comparison with three other specimens of ventral shields of *Tolypelepis* from the Baltic (TUG 68-1 in this work and GIT 168-5 (= Pi 5004) and LIG 25-023 in Märss 1977b). Its anterior right corner is worn and the posterior right quarter (left in the figure) is broken but the outline of the shield is still discernible. The exposed part is 37 mm long and about 20 mm wide. The shield is strongly convex, deeply vaulted (term by Denison 1964, p. 318). The anterior margin is slightly convex, turning smoothly to the lateral and then to the posterior convex margin, giving the shield an elongate oval shape. There occurs a very conspicuous wide (about 3 mm) anteriorly and laterally distributed marginal dentine ridge band of fine parallel ridges, 8 ridges per mm. A preserved antero-lateral corner shows that the ridges of the band are continuous and extend from anterior to lateral. Behind the anterior band there is an area on the shield, where the ridges form a fan-shaped pattern towards the antero-lateral corners. A few tessera-like units can be recognized on both sides of that fan. The tessera-like units are short, with a medial wider and higher ridge, and flanked with 1–2, sometimes up to 4 lower but also narrower side ridges; the length of the units anteriorly on the shield is 1.4–1.8 mm and width 0.9–1.3 mm, while posteriorly on the shield the respective numbers are 2.1–2.3 and 1.4–1.5 mm. Such units are characteristic of the anterior and posterior thirds of the shield. The medial third is covered with relatively lower but also longer units, which in some places are tessera-like but in other places occur as interrupted elongate ridges as is common in the *Tolypelepis undulata* ventral shield. The units enclosing pores of lateral line canals are asymmetrical. The lateral line canal system is of cyathaspidid type but not complete in this specimen (Fig. 6H) where pores of the post-oral canal, medial ventral transverse commissures and the lateral ventral canal can be recognized.

Tolypelepis sp. indet.

Figures 9D, 10F, G

Locality and horizon. Loc. 8825-11/15a, Right Anuchin River, Cape Vize, north of Northern Island, Novaya Zemlya Archipelago; uppermost part of Konstantin Formation, Pridoli, upper Silurian.

Material. Ventral shield fragment GIT 721-5 in visceral view.

Description. The maximum length of the specimen is 12 mm and width 7 mm (Figs 9D, 10F); a small piece of the shield from somewhat farther from the main shield and a slightly lower level (Fig. 10G) is 5 mm long. The anterior margin of the shield is slightly concave, indicating that it is the ventral shield. The moulds of 6–7 tessera-like units resembling those of *Tolypelepis* are exposed in places where the shield is broken away (Fig. 10F, G). There are 7–8 side ridges per mm converging behind the medial ridge seen in the mould; the medial ridge seems to be rather high. The length of the medial ridge in the units is about 3 mm, so, the units are relatively large with a relatively high number of side ridges. The shield partly exposes a cancellous (or honeycomb-like layer), which is characteristic of most cyathaspidid heterostracans.

Besides *Tolypelepis* sp. ind., a 1.2 mm wide ridge covered with fine slanting ridgelets is seen on the right side of Fig. 9D. This may belong either to *Lophosteus*? sp., an acanthodian or a tessellated heterostracan (e.g. *Lepidaspis*-like).

Comparison

Specimens of four species from *Tolypelepis* are available for comparison while *T. undulata* and *T. leopoldensis* also offer ventral shields for that purpose (Table 3).

The ventral shield of *T. bedovensis* sp. nov. is longer than that of *T. undulata* (see Table 3) but just slightly narrower; some flattened specimens of *T. undulata*

Table 3. Comparison of *Tolypelepis* species. Explanations: rec., reconstructed measurement; rostr., measurement on rostral epitegum; ventral measurements underlined; data for *Tolypelepis lenzi* from Dineley & Loeffler (1976) and for *T. leopoldensis* from Loeffler & Jones (1977); size of units for *T. undulata* from Deck (2015)

Taxon	Length (mm)	Width (mm)	Ridges per mm	Size of units (mm)
<i>T. undulata</i>	32–38 <u>32</u>	23 <u>22</u>	Average 4 (2–8) <u>average 4</u>	Length 1.8 (±0.3), width 1 (±0.2) on dorsal shield
<i>T. lenzi</i>	27	20	5–7	Length 1–4, width 1.0 on central epitegum of dorsal shield
<i>T. leopoldensis</i>	35 <u>rec. 36</u>	27 <u>28</u>	7 (4 rostr.) <u>6</u>	Length 2–3, width 1.5 behind pineal region on dorsal shield
<i>T. bedovensis</i>	<u>37</u>	<u>20</u>	<u>4</u>	Length 1.4–2.3, width 0.9–1.5 on ventral shield

(Märss 1977b, pl., fig. 6) may be even wider than shown in Table 3. The ridge width of *T. bedovensis* sp. nov. is rather similar to that of *T. undulata* but bigger than in *T. leopoldensis* and *T. lenzi*. The tessera-like units of the ventral shield of *T. bedovensis* (at least anteriorly) are shorter and narrower than in *T. undulata* (Märss 1977b, fig. 5A–C, pl., fig. 5). The wide marginal band of parallel fine ridges on the ventral shield, which was pointed out for *Cyathaspis* by Denison (1964, p. 318) and is present in *C. alexanderi* sp. nov., brings *T. bedovensis* sp. nov. closer to *Cyathaspis banksi* and *C. acadica* (Denison 1964, figs 110B and 111, respectively). That band in *T. undulata* is narrower and ridges are wider. The lateral line canal pores are very distinct, with rather large openings in *T. undulata* but inconspicuous or not distinguishable in *T. lenzi* and *T. leopoldensis* (Dineley & Loeffler 1976; Loeffler & Jones 1977). In *T. undulata* the lateral line canals occur as short segments on the rostral and central epitega of the dorsal shield and on the ventral shield (Denison 1964, p. 330, fig. 37A; Märss 1977b, figs 1A, 11B).

SUMMARY

The Silurian cyathaspidid heterostracans collected in 1970–2006 were studied. The material described complements the data on the taxonomic content and the spatio-temporal distribution of the species of the family Cyathaspididae. The specimens were obtained from the East Baltic (Estonia, Latvia, Lithuania and Kaliningrad District), the Southern and Central Ural Mountains and their northern prolongation, the Novaya Zemlya Archipelago, and from the remote Severnaya Zemlya Archipelago. *Archegonaspis schmidtii* (Geinitz, 1884), *Archegonaspis lindstroemi* Kiaer, 1932, *Archegonaspis integra* (Kunth, 1872) and *Tolypelepis undulata* Pander, 1856 were recognized and re-described; *Archegonaspis bimarisi* Novitskaya, 1970 is synonymized under *A. schmidtii* (Geinitz) and *Tolypelepis mielnikensis* Dec, 2015 under *Tolypelepis undulata* Pander, 1856. Three new taxa, *Archegonaspis bashkirica* sp. nov. from the Ludlow of the Southern Urals [treated by Obruchev (1938) as *Cyathaspis* sp. ind. and *Cyathaspis*?], *Cyathaspis alexanderi* sp. nov. from the Ludlow or Pridoli of the Central Urals and *Tolypelepis bedovensis* sp. nov. from the Pridoli of October Revolution Island, Severnaya Zemlya Archipelago, were established. Two taxa, *Archegonaspis ?lindstroemi* Kiaer from the Wenlock of Pioneer Island, Severnaya Zemlya Archipelago, and *Tolypelepis* sp. indet. from the Pridoli, upper Silurian of Northern Island, Novaya Zemlya Archipelago, remained in open nomenclature.

The studied material details the morphology of dorsal and ventral shields and partly the branchial plates of *Tolypelepis undulata* Pander, *T. bedovensis* sp. nov. and *Archegonaspis integra* (Kunth), the dorsal shield of *Archegonaspis lindstroemi* Kiaer and branchial plates (a few broken specimens) of *A. lindstroemi*.

It was shown that the sculptural characteristics of dermal shields and plates are decisive in taxonomic work along with the morphological details of plates or without them if the latter are not available. A new subfamily Archegonaspidinae subfam. nov. was created based on the unique ridge pattern on the shields. This subfamily includes the taxa (at present the genus *Archegonaspis* Jaekel) containing at least four species with a specific sculpture on shields and branchial plates different from that of the other genera. They all have long to medium-sized longitudinal ridges running over the head shields and plates except their anteriormost parts; some may have tessera-like units near the posterior end of the dorsal shield (the central epitegum of *A. lindstroemi*).

The studied *Archegonaspis* (subfamily Archegonaspidinae subfam. nov.) has at least four main types of sculpture ridges: (1) rather flat long ridges of uniform shape and almost the same width (*A. lindstroemi*); (2) mainly long ridges, some of them subdivided, in places, into shorter lengths (*A. schmidtii*); (3) wider and higher (stronger) long meandering ridges alternating with a number (1–4) of narrower and lower shorter ridges; the stronger ridges may form twin-ridges (*A. integra*); (4) long and straight ridges forming ridge sets, where three finer ridges occur between two wider ridges (alternation ratio 1:3:1) (*A. bashkirica* sp. nov.). Ridges of types 2–4 have a convex surface. In some species the ridges may run from the anterior end up to the posterior end of the plates (*A. lindstroemi*, *A. bashkirica*).

Two species from the genus *Tolypelepis*, subfamily Tolypelepidinae, have the following characteristics. The ridges form (1) relatively short tessera-like units with a relatively small number of ridges surrounding the medial ones (*Tolypelepis bedovensis* sp. nov.) or (2) somewhat longer units with a relatively high number of ridges surrounding the medial ones (*T. undulata*). In both *T. bedovensis* sp. nov. and *T. undulata* the tessera-like units anteriorly become scale-like posteriorly on the shields, each unit with a narrow overlapping area posteriorly. In the genus *Cyathaspis*, subfamily Cyathaspidinae, (1) the ridges form tessera-like units, which are relatively long and distinct (*Cyathaspis acadica* and *C. banksi*; Denison 1964) or (2) tessera-like units are less distinct but still with a longer and stronger medial ridge and narrower ridges on the flanks (*C. alexanderi* sp. nov.). The length of the units and number of flanking ridges are taxon-specific. Unlike *Archegonaspis* ridges, the ridges do not

run from the anterior end up to the posterior end of the shields/plates.

Ridgelets/indentations on ridge margins are rather common in cyathaspidid specimens. Depending on the position of ridges on the body, the ridgelets occur transversely anteriorly or diagonally posteriorly on the margins of shields and plates. There exist simple single fine ridgelets, double ones, or those of rather irregular distribution (Fig. 3H–M). The character of ridgelets may become useful for future taxonomical studies.

The paper also describes the lateral line sensory system in well-preserved specimens of *Tolypelepis undulata*, *T. bedovensis* and *Archegonaspis integra* which have morphologically similar pore distribution patterns. The lateral line system is formed of closed segments in the shields and plates (Denison 1964; Märss 1977a, 1977b). Pores of supraorbital canals, lateral and medial dorsal canals and dorsal transverse commissures between them, pores of lateral and medial ventral canals and lateral and medial ventral transverse commissures and postoral canal were recognized. The distribution of pores helped to orient and find the location of fragments on the body. Two pores of the lateral line, perhaps connecting the lateral dorsal and lateral ventral canals (branchial transverse commissure), were discovered anteriorly in the branchial plate of *Archegonaspis* (*A. ?lindstroemi*). The appearance of pores anteriorly in the branchial plates needs to be studied in other *Archegonaspis* specimens/species as well but already now they are known in *Poraspis* and *Anglaspis* species figured or mentioned by Stensiö (1958, fig. 166B) and Denison (1964, p. 330).

The variability of scales was studied in the Central Urals *Archegonaspis lindstroemi* as has earlier been done for the East Baltic *Tolypelepis undulata* (Märss 1977b). The results showed that the sculpture features on the shields continued posteriorly on the scales, making it possible to use the scales for taxonomic purposes.

The study also revealed the impressions of internal organs on the visceral side of the dorsal shield of *Archegonaspis schmidtii*, the impressions of the olfactory and pineal organs, semicircular canals and branchial pouches. They are known in several cyathaspidids (see, for example, Denison 1964, figs 106, 131, 132, 151, 155, 156; Novitskaya 2004, figs 23, 25–27, 30). As a new feature, small pits were recognized at the bottom of each hollow, the hollows indicating the impressions of individual exhalent canals of gill pouches.

Differently sculptured patches have been established in the shields of Cyathaspididae. According to Dineley & Loeffler (1976, pp. 104–107), such features as symmetrical oval shape or more complicated configuration

in later growth stages represent the growth lines of the central epitegum of the dorsal shield of *Pionaspis*, *Dinaspidella*, *Poraspis* and *Nahanniaspis* species. In normal ontogeny there was no interruption of the ridge pattern across growth lines. Anomalous areas were produced by interruption of normal growth in species of *Americaspis* (Denison 1964, fig. 160), *Vernonaspis* (Broad & Lenz 1972) and *Archegonaspis* (Novitskaya 1970, pl. 9, figs 1, 2) (in Dineley & Loeffler 1976, pp. 104–107), possibly for both individual and ecological reasons. Elliott & Petriello (2011, p. 523, fig. 5A, B) described a completely different pattern of growth lines on the ventral shield of *Poraspis thomasi* with nine symmetrical, V-shaped anteriorly open markings without any change in the surface ridge pattern. In our material a fragment of the *Archegonaspis lindstroemi* shield (Fig. 3E) has an anomalous unsymmetrical patch at the very end of the shield, which is bounded by a very fine groove from the rest of the shield. The patch is covered by discontinuous dentine ridges. It may be a fractured and healed shield area which here reflects an interruption of normal growth. The reason for fracturing is not known.

Some shields may have healed wounds as found in *Cyathaspis alexanderi* sp. nov. (Fig. 8D, H), distinctly caused by a predator, most possibly by an eurypterid. Rather similar wounds with three puncture marks were described in *Lechriaspis patula* (Elliott & Petriello 2011, fig. 7A, B). The authors presumed that the attack was fatal to this animal as there was no sign of the repair of the damage. Our specimen clearly shows healed ridges in shape of fine tubercles in the pits.

Novitskaya (1970, pp. 112–113, pl. 9, figs 1, 2) described a contrasting patch of dentine ridges in *Archegonaspis bimarisis*, on the primordial zone of the shield. The patch is elongate oval, with longitudinal ridges in its central part and slightly elliptical on the margins. These ridges are narrower (5 per mm) than on the adjacent areas of the central epitegum (4 per mm). According to Novitskaya (1970, p. 111), the ornament of the primordial zone with the presence of lower ridges between the higher ones of *A. bimarisis* shows close relationship with *A. integra*. The difference between these two taxa lies in that *A. integra* has such alternation of ridges on the entire central epitegum, but *A. bimarisis* has it only on the primordial zone, whereas the rest of its central epitegum is covered by rather long and uniform ridges (ibid.).

The study by Greeniaus & Wilson (2003) on the development of the cyathaspidid dermal skeleton during ontogeny showed that its growth and shield formation began at a primordium placed in the posterior region of the shield or scale. The bone formation was cyclomorial,

witnessed by the cyclomorial growth marks on the shield, while the ridge transition into the next growth stage was transitional without interruption. Such concentric growth rings occur in several cyathaspidid shields with a somewhat varying location of the centre (ibid., p. 486).

However, there are still two questionable points concerning *A. bimar*is. (1) The suture between the primordial zone and the rest of the shield is very strong, while according to figures of Greeniaus & Wilson (2003, fig. 1B), it should be smoothly transitional, without the interruption of ridges as in *A. bimar*is. (2) The sculpture patterns on the primordial zone and the rest of the central epitegum of *A. bimar*is are different, having wider and narrower ridges on the primordium (*A. integra* feature) and uniform relatively long ridges with some shorter ones on the rest of the central epitegum (*A. schmidt*i feature). Keeping in mind the development of the cyathaspidid shield by Greeniaus & Wilson (2003), the sculpture patterns on the entire central epitegum should be similar. Nevertheless, the healing of wounds indeed influenced the normal growth of the dermal skeleton on early vertebrates, and is reflected in the surface sculpture, e.g., in anaspid scales [Blom et al. 2002 (for 2001), fig. 30A, C] or other cyathaspidids *A. lindstroemi* (Fig. 3B, E) and *Cyathaspis alexanderi* (Fig. 8D, H) in this work. Therefore, the primordial zone of the dorsal shield in that particular specimen, named as *A. bimar*is, seems to be just an aberrant growth form, and the validity of *A. bimar*is Novitskaya is doubted. The shield morphology of *A. bimar*is, with a smoothly convex anterior margin, a posterior transverse margin without scale-like units, as far as seen, and the uniform ridge pattern, are the features of *A. schmidt*i, even if the size is a bit closer to *A. lindstroemi*. On the basis of the above data, we keep *Archegonaspis bimar*is Novitskaya as a junior synonym of *A. schmidt*i (Geinitz).

The published illustrations of *Tolypelepis mielnikiensis* Dec are of poor quality, especially for the comparison purposes. The study of specimens in Warsaw in 1984 and 1988 by the present author revealed no specific feature that could have served as a basis for establishing a new species. It must be taken into consideration that the perimeter (especially the width of shields) can vary pending on the post-sedimentation processes as well as on the shield construction when the thin and weak interr ridge grooves may become wider or, on the contrary, shrink, changing also the numerical values for us. An example of the influence of such processes on the shield perimeter is the specimens in the limestones of the Ohesaare Cliff, where the *Tolypelepis undulata* shields are three-dimensionally preserved while they are flattened in the marls of the Ruhnu core (e.g. Märss 1977b).

We consider the feature diagnosed ‘as unique due to the rostral region being constricted at orbital level’ (Dec 2015) too weak, and thus *Tolypelepis mielnikiensis* Dec is treated as the junior synonym of *Tolypelepis undulata* Pander herein.

Acknowledgements. I thank the Director of the Department of Geology, Tallinn University of Technology, for providing facilities enabling me to continue my studies on fossil agnathans. M. Isakar (Tartu) is acknowledged for the loan of two *Tolypelepis undulata* specimens; R. Einasto, V. Viira (both Tallinn), R. Sobolevskaya (St Petersburg), A. Poleshchuk, E. Lenkin and A. Khapilin found the new *Archegonaspis* and *Tolypelepis* specimens. R. Sobolevskaya also provided the locality and biostratigraphic data for this study. A. Blicck (Lille), L. Werdelin, T. Mörs (both Stockholm), H. A. Nakrem (Oslo), T. Schossleitner (Berlin), S. Meng (Greifswald) and H.-P. Schultze (Lawrence, USA) helped to resolve the problems concerning the types of *Archegonaspis integra*, *A. lindstroemi* and *A. schmidt*i. I am much obliged to M. V. H. Wilson (Edmonton, Alberta) for helping decipher the ICZN. The expedition fellows T. Modzalevskaya (St Petersburg), A. Zhivkovich and P. Chekhovich (both Moscow) made the expeditions memorable and gave all-round help in the field. A. Ivanov (St Petersburg) took the digital images of D. Obruchev’s specimens and G. Baranov (Tallinn) prepared all other images for publication. K. Ronk (Tallinn) re-drew the scales and M. Märss (Tallinn) digitized all drawings used herein. I thank M. Ginter (Warsaw), H. Blom (Uppsala) and U. Toom (Tallinn) for financing my trip to Poland to the 14th International Symposium on Early and Lower Vertebrates in 2017. Financial support for writing this paper came from my family. I am deeply grateful to the referees of the manuscript D. Elliott (Flagstaff, Arizona) and M. V. H. Wilson (Edmonton, Alberta), whose useful comments and corrections improved the paper. The publication costs of this article were covered by the Estonian Academy of Sciences.

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Põhja-Euraasia Siluri tsüataspäidsed heterostraagid

Tiiu Märss

On käsitletud tsüataspäidseid heterostraake, mis on leitud aastatel 1970–2006 Baltikumi, Põhja-Timaani, Kesk- ja Lõuna-Uuralite ning Novaja ja Severnaja Zemlja saarestike Ülem-Silurist. Varem püstitatud liikidest kirjeldati *Archegonaspis schmidti* (Geinitz, 1884), *Archegonaspis lindstroemi* Kiaer, 1932, *Archegonaspis integra* (Kunth, 1872) ja *Tolypelepis undulata* Pander, 1856. Revideeriti kahe perekonna kahe liigi taksonoomiat, mille juures *Archegonaspis bimarisi* Novitskaya, 1970 paigutati *A. schmidti* (Geinitz) alla ja *Tolypelepis mielnikensis* Dec, 2015 *Tolypelepis undulata* Pander, 1856 alla. Esitati kolm uut taksonit: *Archegonaspis bashkirica* sp. nov., *Cyathaspis alexanderi* sp. nov. ja *Tolypelepis bedovensisi* sp. nov. Kaks taksonit, *Archegonaspis lindstroemi?* Kiaer ja *Tolypelepis* sp. indet., jäid täpsemalt määratlemata. Esitati uus alamsugukond *Archegonaspidinae* subfam. nov. Uuringus on näidatud, et kõrvuti kilpide ja plaatide morfoloogia detailidega võib taksonoomias edukalt kasutada ka skulptuuri omadusi. Kirjeldatud materjal täiendab sugukonna *Cyathaspididae* taksonoomilist koostist ja liikide ajalis-ruumilisi levikuandmeid.