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Protaspis larva of an aglaspidid-like arthropod from the Ordovician of Siberia and its habitat

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ABSTRACT

A fossil larva lacking segmentation of the calcified carapace, closely resembling the trilobite protaspis, has been found associated with other skeletal elements of an angarocaridid *Girardevia* species in the mid Darriwilian of central Siberia. The presence of protaspis larvae in the angarocaridids, generally believed to represent a branch of the Aglaspidida, supports their proximity to trilobites and proves a low position on the arthropod phylogenetic tree but does not necessarily contradict the chelicerate affinity. The cephalic appendages of angarocaridids bore massive gnathobases with detachable spines, closely similar to those known in extant xiphosurans and in their probable Cambrian relatives. The stratigraphic succession of the angarocaridids, their phosphatized cuticle pieces being abundant in the Ordovician strata of Siberia, shows a gradual improvement of mechanical resistance of their carapaces, eventually resulting in a honeycomb structure. The associated benthic mollusc assemblage is dominated with the bellerophontids showing high mortality at metamorphosis and only the limpet-like *Pterotheca*, infaunal bivalves, and scaphopods being able to survive this in a substantial number. This suggests a strong selective pressure from predators equipped with well-skeletonised oral apparatuses able to crush mineralized body covers of their prey. Possibly, these were some of the associated conodonts of appropriate size and co-evolving towards their ability to crush more and more resistant cuticle. Less likely candidates for durophagy are endoceratid or orthoceratid cephalopods. Also the angarocaridids themselves, equipped with robust gnathobases of cephalic appendages, apparently predated on benthic shelly animals.

1. Introduction

Traditionally, early arthropods that bore a needle-like telson were considered relatives of horseshoe crabs. The most completely known such form immediately preceding undoubted chelicerates in geological time is *Aglaspis* from the latest Cambrian. Raasch (1939) claimed that it, like chelicerates, had six pairs of cephalic appendages, the anteriormost allegedly being chelate. Re-examination of the only specimen with appendages preserved *in situ* by Briggs et al. (1979) has resulted in rejection of both these claims. Cephalic endopods are preserved also in *Flobertia* (Hesselbo, 1992), but it remains unclear whether the aglaspidid first appendage pair was chelate or antennate. Taxonomic decisions on affiliation of assumedly related forms have to be based only on general aspects of their tagmation. This refers also to relatives of the Siberian Ordovician arthropod *Angarocaris*. The discovered angarocaridid larva is associated with remains of mature individuals showing aspects of their anatomy significantly different from that of *Aglaspis* (Schmidt, 1886; Tschernyshev, 1945, 1953; Andreeva, 1957; Rosov, 2009). Although not especially helpful in clarifying the phylogenetic position of the angarocaridids, this new evidence enables inference on their feeding behaviour and their place in the Ordovician biotic environment.

Probably the most striking aspect of the Siberian angarocaridids is the rigidity of their cuticle at all ontogenetic stages, including the protaspis-like larva. Mineralization of the cuticle does not protect against swallowing by a soft-bodied predator. As proposed below, it is rather an evolutionary response (a case of 'arms-race'; see Dietl and Kelley, 2002) to selection pressure from predators equipped with mouth apparatuses hard enough to crush hard cuticle (e.g., Kruppert et al., 2017). One may expect that such oral structures have a relatively high fossilization potential. An attempt to identify them among fossils associated with the angarocaridid larva is presented below.

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2. Material and methods

2.1. Geological setting

The fossil larva and juvenile arthropods described here come from the locality II on the left bank of the Stolbovaya River, a tributary of Podkamennaya Tunguska (Fig. 1B). The region is now located near the western margin of the Siberian Platform in the middle of its latitudinal extend, but in the Mid Ordovician this region was in the tropics a little south of the Equator (Fig. 1A). The thickness of particular beds shown here (Fig. 1C) slightly differs from that given by Kanygin et al. (2019) in that the sampled cephalopod limestone bed occurs at the base of the one metre thick Volginian mudstone unit, not near its top. The bed disappears northward within the exposure.

The base of the Volginian is correlated with the mid Darriwilian Baltic stage Aseri on the basis of the assumed global nature of eustatic events (Dronov et al., 2009). Potentially, this can be tested with associated assemblage of conodont elements (SMTable 1, SMFigs 1–3), on which biostratigraphy of the Ordovician is mostly based. Unfortunately, despite the richness of the conodont assemblage (2769 specimens) and its relative taxonomic diversity (12 species), no one of the conodont taxa identified in the sample from the base of Ust'-Stolbovaya Formation represents a lineage with the evolution fast enough to enable its use in geochronology. Most of the species are endemic for Siberia and those with global distribution (*Pseudooneotodus*, *Panderodus* and *Semiacontiodus*) are of little correlative value. The only source of information that can be used in intercontinental correlation is the report on occurrence of *Eoplacognathus reclinatus* in Moskalenko (1984). This would mean that the basal Volginian transgressive event correlates with the Lasnamägian Baltic stage, that is late Darriwilian.

Fragmentary phosphatized arthropod remains were reported by Dzik (1980) based on specimens extracted from the sample of a sandy limestone with coarse quartz grains collected by Tamara Moskalenko in nearby exposure 572 of the Volginian limestone (layer 4-2) on the Kokui (Kukuy) island about 20 km upstream of the Podkamennaya Tunguska River from the Kuzmovka village. According to Andrey Dronov (personal communication 2020) strata younger than the Baykit Sandstone do not crop out on the island now. The sample was probably taken from the exposure V on the right bank of the Podkamennaya Tunguska River about 3.5 km upstream from Kuzmovka village (Kanygin et al., 2019). The rather unlikely alternative is that the exposure accessible in the '70 of the twentieth century has been meanwhile covered with debris.

Also the sample 7670/1a from the Moyero River, highly productive in respect to arthropod phosphatized remnants, was taken by Tamara Moskalenko from the bed 1.2 m above the base of the Kirenian stage, thus slightly younger than that from the Stolbovaya II locality. Whereabouts of the section were given by Moskalenko (1970).

The samples with phosphatized arthropod remains discussed in this paper, youngest in geological age, come from the lower part of the Makarovo Formation near exposure VK744 on the left (western) bank of the Lena River downstream of the village Makarovo (Kanygin et al., 1989). Its acid resistant residue abounds in phosphatic microfossils, mostly disintegrated arthropod carapaces. The fossil assemblage is closely similar to that of the underlying Krivaya Luka Horizon (Dzik, 2015).

2.2. Methods

The specimens described here come from acid-resistant residue of a sandy limestone sample taken for conodonts. They were processed in the routine way, using diluted acetic acid to dissolve the rock and the Franz laboratory electromagnetic separator to enrich the residue.

Most specimens of arthropods described here are preserved as non-deformed three-dimensional internal moulds. Apparently, the skeleton was originally calcified, as pointed out by Rosov (2009). In some cases the cuticle is phosphatized, preserving details of external ornamentation. The latter is well replicated in a negative external mould.

The previous report on phosphatized telson and gnathobasis of mid Darriwilian age from the Kokui (Kukuy) Island (Dzik, 1980, fig. 3; reinterpreted by Dzik, 2015) was based on 5 gnathobases and a few dozens of caudal spines. Much more numerous and diverse material comes from the late Darriwilian

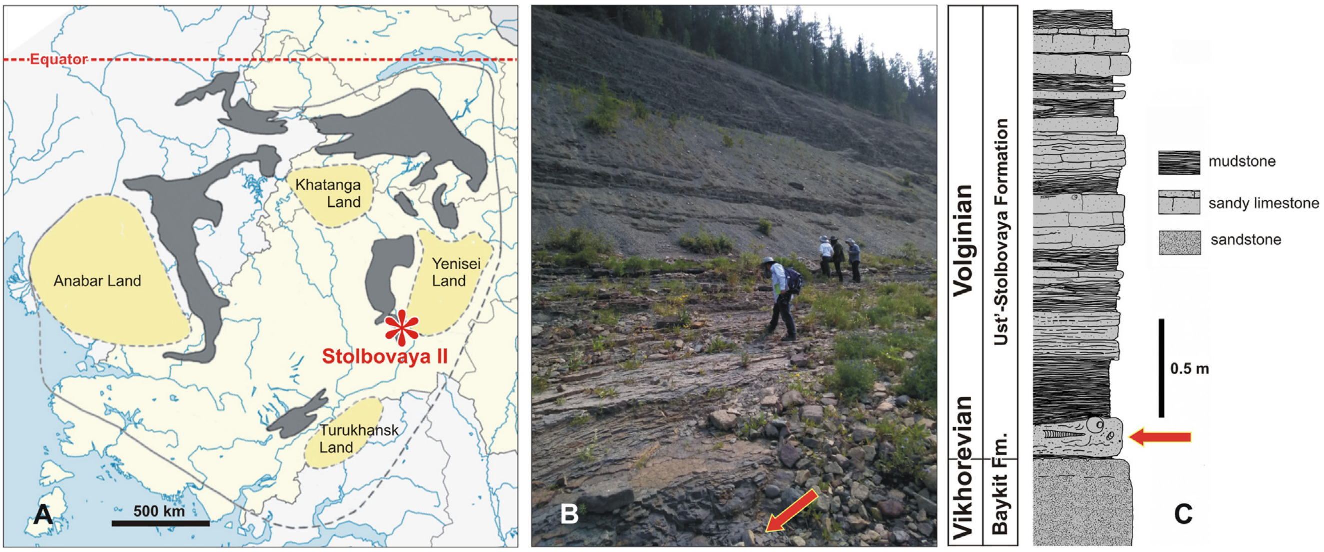


Fig. 1. A. Position of the Stolbovaya II locality (asterisk) on the Siberian Platform in the Darriwillian; exposures of the Ordovician strata shown in grey, hypothetical lands in yellow (based on Dronov et al., 2009; Shatsillo et al., 2017). B. General view of the exposure II on the left bank of the Stolbovaya River; position of the sample indicated with arrow. C. Rock column of the topmost Baikit sandstone and transgressive base of the Ust'-Stolbovaya Formation, both of Mid Darriwilian age.

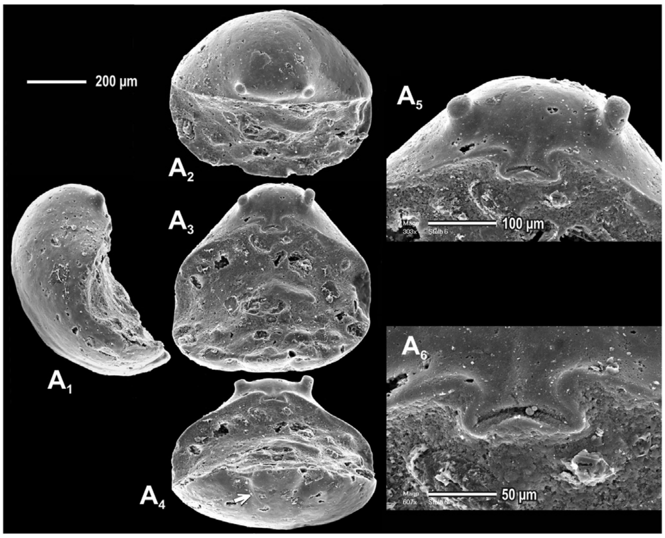


Fig. 2. Internal mould of the protaspis larva of *Girardevia* sp. from the base of Ust'-Stolbovaya Formation at exposure II on the left bank of the Stolbovaya River, specimen ZPAL V.29/6; right lateral (A$_1$), frontal (A$_2$), ventral (A$_3$), and posterior (A$_4$) views and enlarged eyes (A$_5$) and labrum (A$_6$).

of the Moyero River. Numerous fragments of arthropod carapaces were also encountered in conodont samples from strata of late Darriwillian and late Sandbian age (Dzik, 2015) taken by myself at exposures on the Lena River during an expedition in 2007.

SEM photographs were taken of specimens mounted on stubs with a sticky tape and coated with carbon and gold. Whole sets of specimens of bellerophontid gastropod species from the sample were photographed with a digital camera together with a millimetre scale and then measured with ImageJ software.

The collection is housed at the Institute of Paleobiology of the Polish Academy of Sciences (abbreviated ZPAL) in Warsaw.

3. The protaspis larva

3.1. Morphology

The larva found in the acid resistant residue of the conodont sample taken from the base of the Ust'-Stolbovaya Formation at the Stolbovaya II locality is preserved as a phosphoritic mould. It is 0.65 mm long. Its unsegmented body is curved in a way suggestive of being fit into a spherical egg (Fig. 2A1). The carapace is not deformed; the cuticle was apparently stiff. The smooth surface exposed after they were dissolved by acetic acid indicates that the cuticle was calcified. The dorsum is gently convex but the axial part of the body became separated by lateral furrows (arrowed on Fig. 2A$_4$) to develop trilobation near the posterior end. Its tip is broken; so it is not clear if the caudal spine was already developed or not. The anterior margin of the body extends into a Y-shaped prolongation, probably corresponding to the hypostome (Fig. 2A$_6$) attached to the ventral side of the cephalon.

At first glance the Siberian larva resembles the trilobite protaspis stage (Chatterton and Speyer, 1997). That it is not a trilobite is evidenced by the location and shape of its minute eyes (Fig. 2A$_{2, 3, 5}$). They emerge near the margin of the cephalic part of the body and are elevated, with the visual surface gently convex and of an oval outline. Unfortunately, preservation as an internal mould prevents recognition of details. It remains unknown, whether these were compound eyes or just individual ocelli.

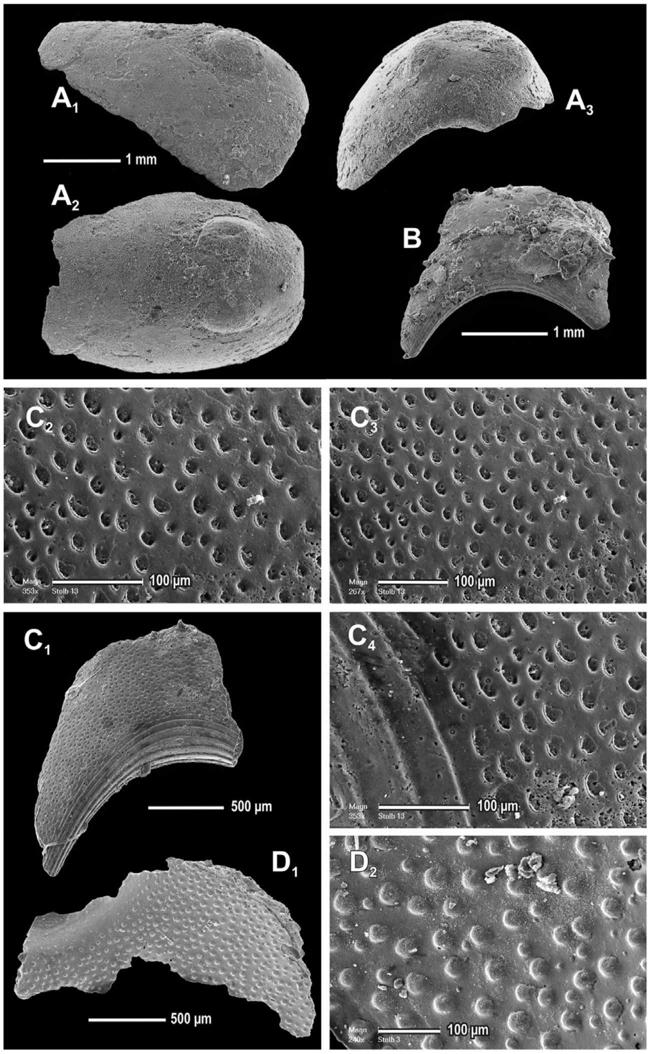


Fig. 3. Pieces of prosoma of *Girardevia* sp. from the base of Ust'-Stolbovaya Formation at exposure II on the left bank of the Stolbovaya River. A. Internal mould of specimen ZPAL V.29/11 presenting anterior an posterior margins intact but not preserved lateral parts; right lateral C and frontal (A$_3$) views. B. Phosphatized fragmentary specimen ZPAL V.29/12 in frontal view. C. Phosphatized fragmentary specimen ZPAL V.29/13 in frontal view l (C$_1$), enlarged punctate dorsal portion (C$_2$ and C$_3$) and the boundary between punctation and terrace lines (A$_4$). D. Phosphatic lining ZPAL V.29/3 of the dorsal surface near an eye (D$_1$) and its enlarged portion (D$_2$) showing that punctae are bluntly terminating pseudopores.

3.2. Taxonomic identity

The frontal position of eyes in the Siberian larva discloses its species identity with associated carapaces of juvenile individuals. All the carapaces in the sample are of the same high-arched shape, elevated anterior tip and kidney-shaped eyes located closely to each other and near the anterior end of the cephalic shield.

Five cephalic shields showing their general appearance are preserved in the Stolbovaya River sample as internal moulds. The only relatively complete one, ZPAL V.29/11 (Fig. 3A), is 3.5 mm long. The flanks of the carapace are almost vertical, like in the slightly younger aglaspidid *Girardevia musculus* Andreeva, 1957 from the middle part of the Ust'-Stolbovaya Formation (Kudrinsk-Kirensk horizon of Late Darriwilian age) of the Angara River (Andreeva, 1957).

Four pieces representing fragments of the carapace anterior margin show parallel terrace lines gradually changing into punctae in the more dorsal parts of the shield. The surface of phosphatized carapaces is covered with terrace lines along their border that gradually change into densely distributed pits covering most of the carapace (Fig. 3C). Negative moulds show that the pits are shallow and terminate as rounded depressions (Fig. 3D).

It is unlikely that more than one species is there represented, although several angarocaridid species are known from the Ordovician of Siberia (Rosov, 2009). Most of them are represented in the fossil material by isolated head shields of mature individuals. This restricts taxonomic considerations to data on their morphology. Two carapaces attributed to *Girardevia*? sp. 2 were reported by Rosov (2009) from the Badaranovo Formation (Vikhorevo Horizon of early Darriwilian age) locality 752 on the right bank of the Vikhoreva River; the more complete of them is 3.35 mm long; that from the late Darriwilian Kirensky Horizon strata exposed in the right bank of Podkamennenaya Tunguska between Gurilevskyi and Gremyachyi Creeks is 4.25 mm long. These are apparently juveniles at the same stage of development as those from the Stolbovaya II sample. The strongly deformed specimen identified by Rosov (2009) as *Girardevia*? sp. 1 from the lower Mamyry Formation (Volgino Horizon of mid Darriwilian age) exposure 753 on right side of the Bratsk—Ust'-Ilimsk highway is 23.0 mm long.

A near-marginal position of eyes closer to each other than it is the case with the remaining Siberian angarocaridids also characterizes the holotype of *Angarocaris czekanowskii* (Schmidt, 1886) from coeval strata exposed near the village Padun on the Angara River (Schmidt, 1886; Tschernyshev, 1945, 1953; Andreeva, 1957). Its second specimen is about 14 mm wide and 8 mm long, large eyes are about 2.5 mm in diameter and the distance between them is 2.5 mm (Tschernyshev, 1953, p. 113). The cephalic shield is crescent-shaped with prominent genal spines but in my specimens genal spines are missing. Both specimens of *A. czekanowskii* are apparently crushed and dorsoventrally compressed (Tschernyshev, 1953, pl. 4:13). It cannot be ruled out that the difference in convexity of the carapace decreased in subsequent ontogeny and/or it is a taphonomic artefact. Until the taxonomic status of the *A. czekanowskii* holotype is clarified, the most parsimonious taxonomc determination of the Volginian species from the Stolbovaya II locality remains *Girardevia* sp.

4. Other angarocaridid skeletal elements

The acid-resistant residues of limestone samples from the Mid Ordovician of Siberia do not yield secondarily phosphatized aragonitic skeletal elements, so typical for the early Palaeozoic ‘small shelly fossils’ assemblages. Mollusc conchs are preserved as internal phosphoritic moulds. Most of the fossils in the samples are originally phosphatic (conodonts) or organic-phosphatic (lingulid brachiopods). Probably the abundant detritus of arthropod cuticles represents the latter category. Whether they were originally phosphatic or whether a certain amount of calcium phosphate in the generally calcitic cuticle promoted its complete phosphatization, remains a matter of dispute (i.a., Lin et al., 2010). The cuticular elements reviewed below are too fragmentary to enable restoration of the whole skeleton. However, they may help in interpretation of more complete fossils with not preserved microstructural details of their morphology.

4.1. Gnathobases

Among phosphatized arthropod cuticular elements found in the Volginian sample from the Stolbovaya II locality there are 32 gnathobases, all with detached teeth (Fig. 4A and B). Antero-basally they extend in a partially preserved lobe that dorsally delimits an oval space presumably corresponding to the subsequent appendage joint.

The Siberian gnathobases are similar to the crustacean mandibles and were erroneously interpreted as such (Dzik, 1980; corrected by Dzik, 2015, p. 30), but they rather belong to the same species as the larva and juvenile carapaces described above. There are no remnants of crustaceans associated with them (except for minute ostracods) that could provide alternative taxonomic affiliation.

Although the caudal spines from the Volginian strata on the Podkamennaya Tunguska Kokuy Island are virtually identical with those from the Stolbovaya river sample, the associated gnathobases are different. They have preserved sclerotised low teeth. Three of them form a transverse row on the presumably distal end, being separated by a diastema from less prominent four more pairs in the proximal narrow half of the gnathobase (Dzik, 1980, fig. 3C).

4.2. Thoracic tergites

Phosphatized pieces of thoracic tergites from the Stolbovaya II exposure represent mostly pleural spines. They are very different from each other in prominence of tips, ranging from those terminating in short sharp spines (Fig. 4C) through elongate rather narrow sharp lobes (Fig. 4D) to rather wide and short terminations (Fig. 4E and F). This seems to reflect a gradient from the angle of the cephalic shield through gradually narrowing tergites of the posteriormost thoracic segments.

Fragmentary specimens from Stolbovaya II are complete enough to enable restoration of the tergite morphology. It appears that pleura were rather thin, with their ventral surface smooth (Fig. 4E) and the dorsal one with oblique terrace lines changing into polygonal pattern closer to the segment axis (Fig. 4F). The axial part of the segment was oval in cross section, strongly elevated both dorsally and ventrally (Fig. 4E and F). The three-dimensionally preserved Siberian material shows that the “anterior tergal process” of Hesselbo (1992) was actually ventral.

The exact number of thoracic (opisthosomal) segments of the Siberian angarocaridids remains to be determined. Rosov (2009, pl. 2:3) presented a specimen of *Angarocaris* with almost complete thorax and telson from the upper Mamyry Formation (Kirensk-Kudrino Horizon of Late Darriwillian age) exposed at the Bratsk–Ust'-Ilimsk highway. There are only 10 thoracic segments on his diagrammatic reconstruction (Rosov, 2009, text-fig. 1) but the specimen is crushed and poorly preserved and one may argue that 11 segments can be counted as well.

The Stolbovaya II collection includes also 36 rectangular sclerites (Fig. 4G) that resemble the last thoracic tergite 13 in the Cambrian possible aglaspidid *Kodymirus* (Lamsdell et al., 2013, fig. 3d). Perhaps the Siberian sclerites belonged to segment 11 or they represent fused ventral plates like those in *Glypharthrus simplex* Raasch, 1939 illustrated by Hesselbo (1992).

Six more enigmatic plates of possible arthropodan identity closely resemble those named *Eurytholia* by Sutton et al. (2001). They are bilaterally symmetrical (Fig. 4H) and may possibly be some medial structures of the angarocaridid skeleton, but I am not able to find any more specific placement for them.

4.3. Caudal spines

Phosphoritic moulds of 87 more or less fragmentary telson spines have been found in Stolbovaya II sample, some with locally phosphatized cuticle (Fig. 4I–N). The proximal end of the spine is characteristic of the species. It faces obliquely to the presumed dorsal side with two lateral lobes constricting the opening and four

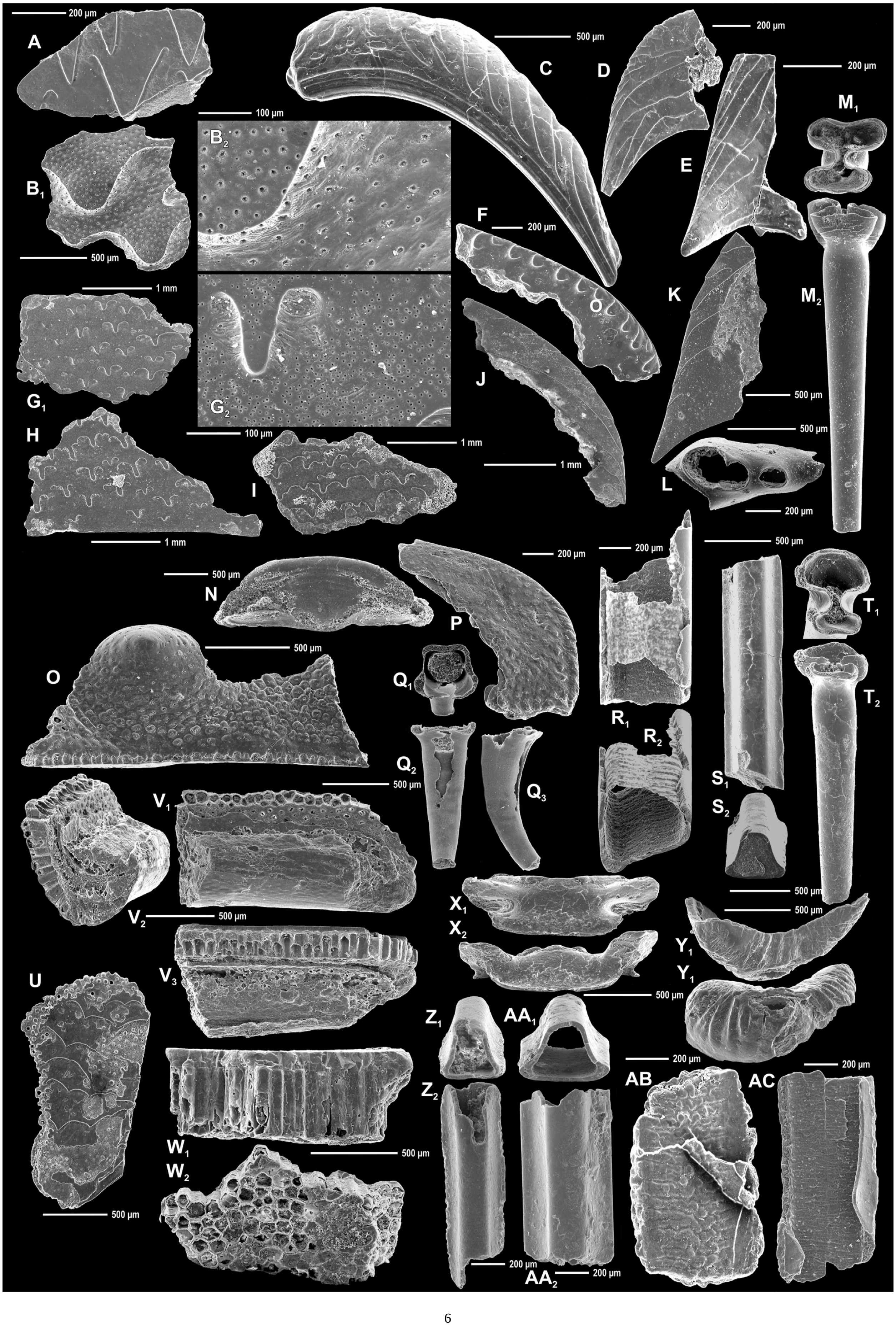
Fig. 4. Phosphatized pieces of the appendages and thoracic tergites of *Girardevia* sp. from the base of Ust'-Stolbovaya Formation at exposure II on the left bank of the Stolbovaya River. A and B. Left gnathobases ZPAL V.29/4 and 5 in occlusal views. C–F. Tergites ZPAL V.29/1, 2, 10, and 9, respectively in dorsal (C,D, F_1, posterior (E_2 and F_2) and ventral (E_1) views. G. Unidentified medial sclerite ZPAL V.29/7 in presumably dorsal (G_1), posterior (G_2), and ventral (G_3) views. H. Enigmatic sclerite *Eurytholia* ZPAL V.29/8 in presumably posterior (H_1) and dorsal (H_2) views. I–N. caudal spines ZPAL V.29/20, 19, 18, 14, 15, and 16, respectively in lateral (I, K_3, L_3, M_3, and N), dorsal ($J_{1, 2}$, L_3, K_2, L_2, and M_2), and anterior (K_1, L_1, and M_1) views.

bulbosities, the dorsal pair of them being a little smaller than the ventral pair. They are ornamented with transverse terrace lines. The remaining surface of the spine was smooth. These tailspines have a slight thickening on the attachment site to the body, which has been observed in various aglaspidids, such as *Aglaspis* and *Grypharthrus* (Hesselbo, 1992; Lerosey-Aubril et al., 2017b). Unfortunately, none of the specimens has its posterior tip preserved.

The specimen from Podkamennaya Tunguska preserved as a phosphatic lining is of the same morphology, despite being associated with gnathal lobes different from those from the Stolbovaya II sample (Dzik, 1980).

5. Diversity of the Siberian aglaspidids

The Siberian aglaspidids were first described by Schmidt (1886) based on two specimens collected by Jan Czekanowski at the locality Padun on the Angara River near Bratsk. The sandstone was believed to be of Devonian age until Tschernyshev (1945) referred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to its dating as the Early Ordovician or Cambrian by S. Obrutchev. The specimens became types of two separate species and genera *A. czekanowskii* and *Chacharejocaris punctata* (Schmidt, 1886) but, despite subsequent extensive research, the angarocaridid taxonomy remains far from being clarified.

The genus *Angarocaris* was introduced by Tschernyshev (1953) for several new species and Novozhilov (1962) choose *Eurypterus* (?) *czekanowskii* Schmidt, 1886 as its type. For some reason the name of species was transcribed into *A.* '*tschekanowskii*' by Tschernyshev (1953), although it is clear from its original spelling, as well as the text preceding description and the plate captions in Schmidt (1886), that his intention was to honour the geologist Jan Czekanowski. Its holotype by monotypy is the specimen described by Schmidt (1886, pl. 2:21—23). There was no need to designate the second specimen, collected by Yu. A. Zhemchuzhnikov between 1920 and 1930 and described by Tschernyschev (1953, pl. 4: 13), the lectotype (actually neotype) of the species, as proposed by Rosov (2009). The prominent cheek spines and relatively flat carapace completely covered with terrace lines are diagnostic for *A. czekanowskii* (Rosov, 2009). According to Andreeva (1957) the strata exposed in the ravine at the village Padun represent the Inteya horizon, which in present-day terms means the Volgino horizon of the mid Darriwilian.

Even more complicated is the nomenclatorial history of *C. punctata*. It was introduced as the new species *C.* '*punctatus*' (incorrect masculine gender of the species name; the same refers to names introduced by Rosov, 2009) by Tschernyshev (1945) on the basis of specimens collected by G.F. Krasheninnikov from a thick-bedded sandstone in exposure 1012 of S.V. Obrutchev on the right bank of the Angara River, 200 m downstream the Zabolotnoye Creek, opposing the upstream end of the Chechenchan Isle (beginning of the Shamanskiy ford). The age of the stratum was determined by S. Obrutchev as Early Ordovician or Cambrian. Andreeva (1957) provided a more precise dating (of the stratum with *Obrutchewia*) as the Kudrino horizon (late Darriwilian) and proposed *C. punctata* of Tschernyshev (1945) to be conspecific with *Eurypterus* (?) *punctatus* of Schmidt (1886). This resulted in both a homonymy and synonymy. She included in *C. punctata* also the specimen collected by S.V. Obrutchev from exposure 889 on the left bank of the Angara River, downstream the Pokhmelnyie Rapids, classified as *A.*(?) *punctata* by Tschernyshev (1953), as well as *A.*(?) *chacharejensis* Tschernyshev, 1953 based on the specimen collected by Yu.A. Zhemchuzhnikov from an exposure near the Panteleyev farmstead.

G. musculus, the type species of the genus *Girardevia* Andreeva, 1957, to which the material from the Stolbovaya II sample is here attributed, was collected by G.A. Kuznetsov in exposure 172 on the left bank of the Angara River at the village Balashovo from a concretion in greenish sandy marls of the middle part of the Krivaya Luka Horizon (Kudrinsk-Kirensk Horizon of Late Darriwilian age according to Andreeva, 1957). It was associated with orthid and rhynchonellid brachiopods (as well as nautiloids) indicating a fully marine environment. Also *G. tungussensis* Andreeva, 1957, collected by O.I. Nikiforova from greenish-gray bedded mudstone in the core of borehole No. 11 drilled in the Gur'ev mineral deposits field on the Podkamennaya Tunguska River, correlated with the middle part of the Krivaya Luka Horizon on the Lena River, was found associated with orthid brachiopods.

Rosov (2009) introduced several new late Darriwilian species with smooth cuticle in all the specimens, in which it is preserved, except for the ornate *Rozhkovocaris inflata* from unit 19 bed 2 in exposure 791 on the Angara River 5 km downstream the village Rozhkovo. Its carapace is covered with rows of punctae in places forming irregularly distributed furrows, somewhat similar to those on carapaces from the Stolbovaya II sample.

The geologically youngest among Siberian aglaspidid described up to date is *Obrutchewia* from the upper part of the Ust'-Stolbovaya Formation (Andreeva, 1957; Rosov, 2009). The original specimens of Tschernyshev (1945, 1953) are strongly sclerotized and presumably secondarily phosphatized.

The limited number of macroscopic fossils of angarocaridids has been supplemented by numerous findings of phosphatized carapace and appendages fragments, although at the moment they cannot be matched with more completely preserved skeletons. For instance, an incomplete gnathal lobe that does not substantially differ from those found in the Volginian strata at Stolbovaya II has been also found in sample 7670/1a from somewhat younger late Darriwilian Kirenskian-Kudrinian strata on the Moyero River (Fig. 5L). The associated 40 more or less completely preserved proximal parts of the caudal spines (Fig. 5M) and 96 probable distal parts (rather indifferent phosphatic tubes, all without the tip), are identical with those from the Stolbovaya and Podkamennaya Tunguska Rivers. However, 20 small carapace fragments show a different ornamentation (Fig. 5G–I). The parallel terrace lines at the anterior margin of the shield (12 fragments) change into V-shaped 'scales' of the kind occurring in eurypterids and some ceratiocaridid archaeostracans, and then this ornament transforms into punctuations. In places the 'scales' developed rounded tips. The sample yielded also 18 enigmatic possible rectangular sclerites (Fig. 5N). 42 tips of tergite pleura from the sample are of a more uniform shape than those from Stolbovaya II. Apparently, this material represents a different angarocaridid taxon.

One specimen of probable angarocaridid telson spine from the Moyero River sample, unfortunately with truncated tips precluding its reliable identification, is gently curved. This may suggest affinity of the enigmatic coniform fossils from the late Sandbian or Katian Makarovo Formation exposed at Makarovo on the Lena River (Fig. 5Q), already mentioned by myself (Dzik, 2015, p. 30).

The type locality of *G. musculus* (Andreeva, 1957) has yielded both the telson spines and cuticle fragments with 'fish scale' ornamentation similar to those characterizing the Moyero River and Makarovo species (Fig. 5A–F). Tips of tergites, similarly ornamented with terrace lines, are sharply pointed. The assemblage includes also a single specimen of the third kind of probable telson spines with a trapezoidal cross section and thick walls build of paired sets of narrow transverse chambers, better represented in localities of somewhat younger geological age.

Fig. 5. Succession of phosphatized skeletal debris of taxonomically unidentified angarocaridids in the post-Volginian strata of Siberia. A–F. Calcareous concretion in mudstone of the late Darriwilian Krivaya Luka. Formation at Balashevo on the Lena River, the type horizon of *Girardevia musculus* Andreeva, 1957. A, B. Carapace fragments ZPAL V.29/119 and 120. C. Anterior margin of the carapace ZPAL V.29/122. D–F. Tips of pleurae ZPAL V.29/12, 124, and 121. G–N. Sample 7670/1a taken 1.2. m from the base of the latest Darriwilian Kirensk beds on the Moyero River. G–I. Carapace fragments ZPAL V.29/97, 96, and 96. J, K. Tips of pleurae ZPAL V.29/104 and 103. L. Gnathobasis with spines detached ZPAL V.29/101. M. Caudal spine ZPAL V.29/100. N. Probable abdominal sternite ZPAL V.29/102. O–T. Katian (or Sandbian) Makarovo Formation at Makarovo on the Lena River. O. Lateral margin of the carapace ZPAL V.29/114. P. Tip of pleura ZPAL V.29/115. Q. Internal mould of stacked probable caudal spines with tetragonal cross section showing thickness of the dissolved, originally calcareous wall of the inner spine. R—S. Probable caudal spines with trapezoidal cross section ZPAL V.29/116 and 118. T. Telson spine ZPAL V.29/117. U–AC. Makarovo Formation at Zaborie on the Lena River. U. Carapace fragment ZPAL V.29/106. V, W. Carapace fragments with honeycomb structure ZPAL V.29/111 and 108. X. Probable abdominal sternite ZPAL V.29/113. Y. Gnathobasis ZPAL V.29/112. Z–AC. Probable caudal spines with trapezoidal cross section ZPAL V.29/107, 109, 105, and 110.

Spines of similar morphology are common in the Makarovo Formation exposed at Makarovo and Zaborie on the Lena River (Fig. 5R and S, Z–AC). Unfortunately, both ends are truncated in all specimens collected. Possibly, these spines match the carapace fragments with the wall of honeycomb structure (Fig. 5V and W) imitating that of some pteraspidid agnathans (Keating et al., 2015) or beetle elytra (Yu et al., 2020). There the exocuticle is finely laminated, with the lamina thickness about 3.7 μm, but the endocuticle forms polygonal, highly regular vertical chambers 0.08–0.09 mm in diameter. The cephalic shield margin was ornamented ventrally with parallel terrace lines and laterally with rows of large tubercles (Fig. 5O). Telson spines similar to those of the Darriwilian *Girardevia* occur at Makarovo as well, although differing in having a much narrower dorsal set of proximal bulbosities in comparison to the ventral one (Fig. 5T).

Both at Balashevo and Makarovo rounded tergite tips with prominent tuberculation (Fig. 5F, P) have been found. They are difficult to match with co-occurring skeletal remains. This shows that in the course of evolution of the Siberian angarocaridids their morphological diversity strongly increased, with at least three supraspecific rank taxa developed before the Late Ordovician. The general tendency was to develop a thicker, more rigid, mineralized skeleton. Such anatomical transformation suggests a strong selective pressure from predators.

6. Affinities of the angarocaridids

Siberia was probably the centre of diversification of the angarocaridids in the Mid and Late Ordovician and improving properties of their exoskeleton. Strong enough calcification of the cuticle to enable three-dimensional preservation of carapaces in sandstone or limestone matrix characterizes also the Late Ordovician *Gogglops* from the Chinese Yaoxian Formation (Siveter et al., 2018). It is a member of diverse trilobite, brachiopod, and nautiloid assemblage similar to that from the basal Ust'-Stolbovaya Formation. In having marginal trilobite-like limbs, *Gogglops* resembles the geologically youngest Siberian aglaspidid *Obrutchewia* from the upper part of the Ust'-Stolbovaya Formation (Andreeva, 1957; Rosov, 2009). The strong mineralization of the carapace of both these Siberian and Chinese arthropods, their occurrence in open-sea environment, and the presence of robust gnathobases at least in Siberia, suggest that they together form a separate clade. The lack of evidence on the composition of the cephalic shield is the fatal shortcoming of any attempt to clarify a more general evolutionary position of the angarocaridids. As a result, they tend to be removed from considerations (Ortega-Hernández et al., 2013; Lerosey-Aubril et al., 2017a). Until it is determined whether the first cephalic appendages were tactile-olfactory antennae or rather grasping chelicerae, this must remain an informal taxonomic unit.

The presence of a caudal spine has appeared to be of limited value in high-level taxonomy. The oldest undoubted caudal spine-bearing chelicerate with a determined number and morphology of cephalic (prosomal) appendages is the mid Silurian *Dibasterium* (Briggs et al., 2012), which preserved a primitive form of opisthosoma, that is freely articulated between all the opisthosomal segments. However, in the Cambrian *Emeraldella* (Stein and Selden, 2012; Lerosey-Aubril and Ortega-Hernández, 2019; Liu et al., 2020) a spine-like telson was associated with four pairs of cephalic appendages and trilobite-like filiform antennae. Also *Aglaspis* and its probable relative *Kodymirus* from the Early Cambrian of Bohemia, remain at a low level of cephalisation having just four pairs of cephalic appendages (Briggs et al., 1979; Lamsdell et al., 2013). The most apparent difference of the aglaspidids from typical trilobites (but not the olenellids) and similarity to chelicerates is the absence of dorsal ecdysial sutures and the tail spine (Ortega-Hernández et al., 2013; Van Roy, 2005; Ortega-Hernández et al., 2016; Lerosey-Aubril et al., 2017a). Unlike both trilobites and early chelicerates, the opisthosomal appendages of *Aglaspis* were uniramous. However, the *Khankaspis* from the Snegurov series of the Khanka Terrane on the Pacific shore of Siberia, show exopodites with a complex multiblade organization (Repina and Okuneva, 1969). Although I had an opportunity to examine the original specimens, they are so crudely phosphatized that they hardly offer any taxonomically relevant data. Its exact age remains unknown but the terrain, on which they were collected, was probably close to North China in the Early Palaeozoic, which may explain its similarity to the Chinese *Gogglops*.

The most completely preserved angarocaridid is *Intejocaris maxima* Tschernyshev (1953) collected by S.V. Obrutchev at his locality 906 on the Intey Island on the Angara River from strata probably coeval with those exposed near Padun. It had at least 12 abdominal segments (possibly 13) and a needle-like telson (Tschernyshev, 1953, p. 120). The telson and most of the abdominal segments (10) are also preserved in *Angarocaris*(?) *exsculpta* Tschernyshev, 1953 collected at the same locality by S.V. Obrutchev. The telson is triangular and wider in cross section in its proximal part. It shows ventrally a fish-scale ornament (Tschernyshev, 1953, p. 115). The tip of the tail spine in *G. simplex* Raasch, 1939 from the Furongian was forked (Hesselbo, 1992) like that of the Silurian synziphosurine *Dibasterium* (Briggs et al., 2012). The tagmation of *Glypharthrus* suggests that the segment 12 was incorporated into the aglaspidid tail spine (Lerosey-Aubril et al., 2017a).

It is now generally believed that not the aglaspidids but rather 'the great appendage arthropods' were ancestral to the chelicerates (Dunlop, 2010; Ortega-Hernández et al., 2016). Among them is the Cambrian *Leanchoilia* (Aria et al., 2015) with its earliest known larval stage being already relatively advanced in developing tagmation and differentiation of appendages (Liu et al., 2014). It does not resemble the horseshoe crab 'trilobite larva' and also the mature cephalon of *Leanchoilia* is still at the trilobite stage of cephalization, with four pairs of the cephalic appendages.

Assuming that the anatomy of *Aglaspis* is representative for its whole taxonomic unit, there are important differences in the cephalic appendage structure between them and the angarocaridids. Their carapace was rather weakly sclerotized and there is no evidence for its mineralization. Both the prosomal and opithosomal appendages of *Aglaspis* were uniramous and there is no apparent stronger sclerotisation of their gnathobases (Briggs et al., 1979).

The presence of robust gnathobases with strongly cuticularised teeth (spines), which tend to be detached in early angarocaridids (Fig. 4A and B, 5L) and probably developing a molar appearance in advanced forms (Fig. 5Y), makes them different from *Aglaspis* and similar rather to the extant xiphosuran *Limulus*, as well as to the Cambrian probable ancestors of chelicerates (Aria and Caron, 2017; Bicknell et al., 2017). Strongly sclerotized teeth of gnathobases are common among Cambrian megacheiran arthropods with spatulate telson (Jago et al., 2016; Zakaï et al., 2016; Bicknell et al., 2017). In *Sidneyia* (classified as a vicissicaudatan by Ortega-Hernández et al., 2013; Stein, 2013, and Lerosey-Aubril et al., 2017a) the gnathobasic spines are as strongly thickened and morphologically distinct from the remaining gnathobase, as is the case with the extant *Limulus* (Bicknell et al., 2018). They had different fossilization potential than the rest of cuticle, which resulted in their occasional separate preservation (Bicknell et al., 2017). This explains their detachment from the gnathobases of Siberian angarocaridids.

The spinose strongly sclerotized gnathobases are known also in the Cambrian *Habelia*, truly close anatomically to chelicerates in having six pairs of cephalic appendages (Aria and Caron, 2017). The anteriormost pair of reduced raptorial appendages is possibly homologous with chelicerae. *Habelia* had a prominent tail spine and 12 opisthosomal tergites. Somewhat troublesome in the context of probable chelicerate affinities are its pedunculated eyes. They were inserted in incisions in the head shield, which may be the stage in their incorporation in the prosoma (Aria and Caron, 2017).

Such widespread occurrence of gnathobases armed with thickened spines suggests that this is a plesiomorphic character for arthropods (Bicknell et al., 2017).

7. Possible predators on angarocaridids

The apparently thick calcitic carapace of the Siberian angarocaridid protaspis larva implies a selection pressure from a predator of appropriate body size. Strongly sclerotized 'teeth' of gnathobases in adults indicate that they themselves were durophagous predators (Bicknell et al., 2018). To crush a skeleton impregnated with calcium carbonate requires that the predator is equipped with an equally rigid mouth apparatus. Therefore, even if evidence on the Ordovician soft-bodied organisms is very limited, one may expect that both the animals predating on the angarocaridid larvae and those predated by mature angarocaridids are represented among skeletal fossils identified in the sample Stolbovaya II. At least two groups of invertebrates, along with the angarocaridids, can be considered as the selective factors: conodonts and nautiloid cephalopods. In the Supplementary Material, I review the taxonomic composition of the nekton and benthos associated with the angarocaridids in an attempt to identify species connected with them in the food chain.

Conodonts were mostly a few centimetre sized animals of lamprey-like morphology, which for more than three hundred million years significantly contributed to marine fossil assemblages. Their oral apparatus teeth (elements) were composed of hydroxyapatite, thus of a resistance similar to vertebrate tooth enamel. An intriguing aspect of their biology is that these teeth were frequently broken in action and subsequently regenerated (e.g., SMFig. 2D). This means that their prey was covered with a very hard skeleton. Their association, in absence of other skeletonised predators, in low-diversity fossil assemblages with the angarocaridids, gradually increasing resistance of the exoskeleton, suggests a predator-prey relationship.

If compared in size with the angarocaridid larva, all the conodonts represented in the sample by oral apparatus elements (SMFigs 1–3) could afford to swallow it. However, none of the conodont species present in the earliest Volginian of Stolbovaya II was large enough to crush the carapace of an adult angaricaridid. Truly robust apparatuses emerged later with the distomodontid *Moskalenkodus* (Dzik, 2015). Its presumed ability to crush shells and relatively large carapaces may be connected with the development of thicker carapaces in the angarocaridids, up to the Sandbian honeycomb mineralized cuticle structure (Fig. 5V, W). One may consider this to be a case of co-evolution in an 'arms race' between the predator and its prey (e.g., Dietl and Kelley, 2002; Dietl, 2003; Bicknell et al., 2018).

The only other possible lineages of predators recognized in the Ordovician of Siberia (putting apart possible cannibalistic behaviour of the angarocaridids) are nautiloid cephalopods. Their fossilized conchs are common throughout the Volginian portion of the Ust'-Stolbovaya Formation. These are mostly pseudorthoceratids and endoceratids. Nothing is known about the diet of Ordovician nautiloids, but a Late Carboniferous pseudorthoceratid from the classic Bear Gulch locality of Montana had a strongly sclerotised jaw apparatus (Landman and Davis, 1988). It was probably organic, but its Silurian relative had an aragonitic operculum possibly homologous with jaws (Turek, 1978; Stridsberg, 1984; Holland et al., 1978). It is functionally distant from the beak-like jaws of extant *Nautilus* and its ability to crush carapaces is unlikely.

The biology of endoceratids remains an enigma, it is even not known if the siphuncular deposits were of enough weight to make position of the buoyant conch horizontal. As no mouth apparatus has been found associated with endoceratid conchs, it has been suggested that these nautiloids had a passive mode of life and fed on plankton (Mironenko, 2018). In any case, these were truly large animals and the small-size angarocaridids were hardly of importance in their diet.

8. Shelly animals possibly predated by adult angarocaridids

The sampled rock at Stolbovaya II is full of calcitic brachiopod shells, pieces of crushed large trilobite carapaces (probably a species of *Isotelus*), fragmentary *Sphenothallus* tubes, and probable hyoliths. Unfortunately, the brachiopod shells are invariably split in the middle of their thickness not exposing details of the shell exterior or interior, which prevents their taxonomic identification. Apparently, the most common is an undetermined strophomenid species. The acid resistant residue contains internal phosphoritic moulds of trilobites and bivalves, but especially abundant are gastropod conchs.

Cheek spines of an undeterminable pelagic remopleuridid trilobite are common in the sample. Macroscopic pieces of large trilobite carapaces with terrace lines probably represent *Isotelus*. They are of a size comparable with co-occurring carapace fragments of adult angarocaridids that differ from them in being ornamented with punctae. Their exact dimensions cannot be determined but the carapaces of both trilobites and angarocaridids were definitely of several centimetres width, such as *Intejocaris* (Tschernyshev, 1953). This may be an expression of the evolutionary 'escape in size' to avoid large predators (e.g., Holmes et al., 2019).

The most numerous among molluscs are discoidal conchs with acute venter probably representing the bellerophontid *Trematodiscus*. Its population dynamics shows a prominent peak of mortality at metamorphosis (SMFig. 5A), indicated by a change in the conch geometry from open-umbilicate to discoidal, and very few juvenile postlarval specimens. Assuming that mature conchs were of a size similar to species of *Trematodiscus*-like bellerophontids from other regions, adults are missing in the Stolbovaya II sample. This suggests that the local environment on the sea bottom was not suitable for adults of this species.

No adults have been encountered, like in the 'small shelly fossils' of the Baltic Ordovician (Dzik, 1994, 2020), also in case of a bellerophontid larval conch with a flat dorsum (SMFig. 5A); the postlarval stage had flattened flanks but an acute venter suggesting an affinity to *Tropidodiscus*.

Despite larval conchs of similar shape, the life style of the limpet-like *Pterotheca* was very different. Its size frequency distribution shows a peak of mortality at metamorphosis as well (SMFig. 5B), but the majority of specimens are postlarval juveniles with thick conch walls. Very few specimens show complete apertures but in all of them the external whorl is preserved. This means that predation, if it was the cause of death, did not result in complete destruction of the conch. Presumably, *Pterotheca* was an Ordovician analogue of present-day limpets, difficult to catch by a predator owing to its thick shell of a cap-like shape. There are many examples of evolution of molluscs under a pressure from predators in the fossil record (recently reviewed by Dietl, 2003).

The infaunal scaphopods and bivalves from the Stolbovaya II sample were apparently almost immune of predation. All specimens of the probable scaphopod *Rhytiodentalium* are of similar, presumably mature size. The same refers to juvenile nuculid bivalves, all preserved as articulated shells. This means that an abiotic factor, not predation, was responsible for their sudden death. Hidden under the mud they were out of reach for the angarocarid gnathobases.

9. Conclusions

The early ontogeny of angarocaridids was closely similar to that of trilobites and presumably plesiomorphic for all arthropods. The first stage immediately after hatching was a free-living animal corresponding in development of segmentation to the crustacean nauplius. Unlike the nauplius, it was not planktonic and, as suggested by calcified carapaces, stood under selective pressure from predators able to crush the carapace. Possibly, these predators were conodonts in the open marine environment of the oldest known Darriwilian angarocaridids.

The extant xiphosurans, that are analogues of the angarocaridids in respect to their external morphology (although not necessarily their relatives), lay fertilized eggs in nests buried in sand above the water line (e.g., Ferrari et al., 2011). The developing embryos are thus protected against predation by marine animals for four embryonic molts until hatching (e.g., Funch et al., 2016). They completely depend on the yolk. In fact, lecithotrophy is a common phenomenon among unrelated invertebrates and developed also in some Cambrian trilobites (Laibl et al., 2017). For the majority of trilobites, as well as for the angarocaridids, the main source of matter and energy was the food available on the sea bottom, probably beginning from the first instar. Obviously, also the ancestor of chelicerates had post-hatching stages less derived than the lecithotrophic ‘trilobite larva.’

Among advanced aspects of the angarocaridids that may argue for their proximity to chelicerates rather than to trilobites is the robust appearance of gnathobases. This makes them different from at least *Aglaspis* but similar to the Cambrian habeliids, having the cephalic tagma at the chelicerate grade (Aria and Caron, 2017).

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Appendix A. Supplementary data

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