A new Early Devonian antiarch placoderm from Belarus, and the phylogeny of Asterolepidoidei

DMITRY P. PLAX and ERVINS LUKŠEVIČS


A new asterolepidoid antiarch, *Sherbonaspis talimaae* sp. nov., is described based on the disarticulated skeletal elements from several boreholes in Belarus, from the Lepel Beds of the Vitebsk Formation, which has been assigned to an Early Devonian, late Emsian age. New information is provided on the structure of the paranuchal plate previously unknown in *Sherbonaspis*. Data on the remains of the other fossil vertebrates, and the characteristics of the fossil-bearing rocks are provided. These data add information on the taxonomic composition of the late Emsian–early Eifelian fish fauna from the western part of the East European Platform. The new cladistic analysis of the Euantiarcha provides results more reliable in comparison with the analysis of all antiarchs together, and supports traditional subdivision of the group into Bothriolepidoidei and Asterolepidoidei. However, further analysis demonstrates unresolved polytomy close to the base of the Asterolepidoidei, and supports the hypothesis that the family Pterichthyodidae is polyphyletic. Until the phylogenetic relationships of Asterolepidoidei are more clearly resolved, *Sherbonaspis* is attributed to Pterichthyodidae.

Comparison of the sections of the Lepel Beds of Belarus with the age-equivalent deposits in Estonia, Lithuania, and Latvia supports a late Emsian or possibly early Eifelian age for the Lepel Beds.

Key words: Placodermi, Asterolepidoidei, phylogeny, Devonian, Belarus.

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Introduction

The first findings of antiarchs from probable Lower Devonian deposits on the territory of Belarus were reported almost half a century ago (Bessonova et al. 1972; Lyarskaya 1978; Golubtsov et al. 1983). Published data show that unidentifiable individual scales and fragmentary plates of Antiarcha gen. et sp. indet. have been found in the Obol and Lepel Beds of the Vitebsk Regional Stage, probably corresponding to the upper Emsian, together with stromatolites, plant remains, miospores, conchostracans, ostracods, lingulids, various skeletal elements of arthrodires, scales and fin spines of acanthodians, and teeth and scales of sarcopterygians and actinopterygians. However, for over 20 years there were no new published reports on antiarch remains in the upper Emsian deposits on the territory of Belarus.

Dmitry P. Plax started a new study of the upper Emsian–lower Eifelian deposits in Belarus in 2002. Since then, a large number of wells that intersect these deposits have been viewed and studied. In the cores of some of these wells, he managed to find a few remains of antiarchs, represented by separate small fragments of plates from the proximal segment of the pectoral fin, small fragments of articular processes, and small fragmentary unidentifiable plates and scales. All this small, fragile, highly fragmentary and difficult to determine skeletal material was identified as Antiarcha indet. in a series of publications (Plaksa 2007, 2008; Plax 2008, 2015a, b, 2016, 2018). However, after many years of study DPP was at last lucky to find several well-preserved plates of a new representative of antiarchs, for which we provide a detailed description, and also discuss the phylogeny of euantiarchs, and biogeographic and stratigraphic implications of this new antiarch.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:B5470082-7D5C-461A-BD9F-9A02C2ADFA4D.
Material and methods

The holotype of *Sherbonaspis talimaae* sp. nov. was collected from the grey siltstone of the Lepel Beds reached in the Osipovichi 6 borehole in the central part of Belarus. The other skeletal remains are represented by isolated complete or almost complete armour plates sampled from three wells: Osipovichi 6, Korma 1 and Smol’ki 6п (Fig. 1, Table 1). The specimens were extracted by dissolving rock samples with 9% acetic acid. The preservation of skeletal material is good; it bears no signs of corrosion or abrasion.

The plates were measured using a ruler and Vernier caliper. The skeletal elements were examined under an MBS-1 microscope and photographed with a PowerShot SX130 IS and Sony A58 with an Industar-50 lens. The photographs were processed using Adobe Photoshop CC 2019 and the drawings were constructed using CorelDraw Graphics Suite 2019. Cladistic analyses were performed using the heuristic algorithms of PAUP version 4a (169) (Swofford 2003). The resulting most parsimonious trees were resampled over 100 replicates to generate bootstrap supports for each estimated node. The terminology for morphological characters defined and used by Stensiö (1948), and modified by Miles (1968) and Young (1988), is adopted here. All specimens are stored at the Belarusian National Technical University in the Department of Mining Works, Paleontological Collection, Minsk.

Geological settings

All of the described material comes from the upper part of the Vitebsk Formation, corresponding to the Lepel Beds, Vitebsk Regional Stage. These deposits are quite widespread in Belarus. According to the current Devonian stratigraphic chart of Belarus (Obukhovskaya et al. 2010) the Vitebsk RS completely corresponds to the upper Emsian, Lower Devonian (Fig. 2). However, earlier the same authors placed the Emsian/Eifelian boundary approximately in the middle of the Lepel Beds, close to the boundary between the lower and upper members (Kruchek et al. 2001: fig. 5.22). In the territory of Belarus rocks of the Lepel Beds concordantly overlap deposits of the Obol Beds of the Vitebsk RS and are covered everywhere with deposits of the Adrov RS corresponding to the Middle Devonian Eifelian Stage. Deposits of the Lepel Beds correspond to the upper part of the *Rhabdosporites mirus–Gneudnaspora divellomedium* Miospore Zone, while in terms of conodonts they roughly correspond to the upper part of the *Polygnathus costatus patulus* Zone of the previous version of conodont zonation (Obukhovskaya et al. 2010). However, as conodonts have not been found in the Vitebsk Formation, correlation with the conodont zonation is uncertain. In the Baltic States, the age analogue of the deposits of Lepel Beds is approximately the upper part of the *Rēzekne* Formation (Lyarskaya 1978; Lyarskaya and Kleesment 1981; Obukhovskaya et al. 2010). The upper part of the *Rēzekne* Formation in

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Plate</th>
<th>Borehole</th>
<th>Depth [m]</th>
</tr>
</thead>
<tbody>
<tr>
<td>BNTU 44/2-1</td>
<td>AVL</td>
<td>Osipovichi 6</td>
<td>113.8</td>
</tr>
<tr>
<td>BNTU 44/2-2</td>
<td>PVL</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BNTU 44.1-13a</td>
<td>Pn</td>
<td>Osipovichi 6</td>
<td>118.8</td>
</tr>
<tr>
<td>BNTU 121/20-1</td>
<td>AVL</td>
<td>Korma-1</td>
<td>317.5</td>
</tr>
<tr>
<td>BNTU 158/1-1</td>
<td>PVL</td>
<td>Smol’ki 6п</td>
<td>474.0</td>
</tr>
</tbody>
</table>
the modern stratigraphic chart of Latvia corresponds to the lowermost Eifelian (Lukševičs et al. 2010; Lukševičs and Stinkulis 2018), but to the uppermost Emsian in the stratigraphic chart of Estonia (Mark-Kurik and Põldvere 2012). In Central Russia, the upper part of the Novobasoovo Beds of the Ryazhsk RS may correspond to the Lepel Beds (Rodionova et al. 1995; Valiukevičius and Kruchek 2000; Vorotnikova et al. 2011). As the exact correlation of the Lepel Beds with the global chronostratigraphic scale remains controversial, broader aspects of the Emsian/Eifelian boundary in the Baltic-Belarusian area are considered in the Discussion section. Here we give more details of the locations of the described skeletal elements, the lithological characteristics of the host rocks and a list of fish taxa found together with *Sherbonaspis*.

In Osipoviči 6 borehole, drilled within the Bobruisk buried ledge, at a depth of 118.8 m, a right Pn plate of *Sherbonaspis talimaae* sp. nov. BNTU 121/20-1 was obtained in a greenish grey, dense, platy, silty silt-like clay. Together with it, in this rock and at the same depth, very small indeterminate fragments of Placodermi indet. plates, disarticulated scales of *Cheiracanthus* sp., *Cheiracanthus brevicostatus* Gross, 1973, numerous tooth fragments of Onychodontiformes indet., Sarcopterygii indet., and fragmentary scales of Porolepiformes indet. were discovered. In addition to the remains of the fish listed above, miospores were also found here.

Borehole Smol’ki 6n is situated in the territory of the Surazh buried protrusion of the Voronezh Antecline. The left PVL plate BNTU 158/1-1 has been found in a light grey, fine-grained, well cemented platy quartz sandstone with small admixture of clay. Two small fragmentary plates of psammoid heterostracan, several scales of *Acanthodes* sp., fragmentary scale of Onychodontiformes indet., some small teeth of Onychodontiformes indet. and Sarcopterygii indet. were found in the same sandstone at the same depth. Miospores were found along with the vertebrates.

### Systematic palaeontology

**Euantiarcha Janvier and Pan, 1982**

**Asterolepidoidei Miles, 1968**

**Pterichthyoidae Stensiö, 1948**

**Genus Sherbonaspis Young and Gorter, 1981**

*Type species:* *Sherbonaspis hillsi* Young and Gorter, 1981, Goodradigbee valley near Wee Jasper, New South Wales, Australia; ?Emsian/Eifelian, Lower/Middle Devonian.

**Sherbonaspis talimaae* sp. nov.  

**Figs. 3–6.**

2008a Antiarcha gen. nov.; Plaksa 2008a: 84.  
2008 Antiarcha gen. nov. Plax; Plax 2008: 70, table 1, p. 76.  
2015a Actinolepididae gen. indet.; Plax 2015a: 171, pl. 1: 5.  
2015b Antiarcha gen. nov. Plax; Plax 2015b: 21, table (pars), pl. 1: 10.  
2015 Antiarcha gen. nov. Plax; Plax 2015b: 21, table.  
2018 Antiarcha gen. nov. Plax; Plax 2018: 409.

**ZooBank LCID:** urn:lsid:zoobank.org:actD051501D-F1DA-4EE9-B648-537AB4ED18B0
Etymology: In honour of Valentina Karatajūtė-Talimaa (Vilnius, Lithuania), who recently passed away (1930–2022), in appreciation of her works on antiarchs and thelodonts.

Holotype: BNTU 44/2-2, left PVL plate.

Type locality: Borehole Osipovichi 6, 113.8 m deep, close to Osipovichi town, Mogilev Region, Belarus.

Type horizon: Lepel Beds, Vitebsk Regional Stage, probably upper Emsian, Lower Devonian.

Material:—Right Pn plate (BNTU 44/1-13a), left AVL plate (BNTU 121/20-1), fragmentary right AVL plate (BNTU 44/2-1), left PVL plates (BNTU 44/2-2, BNTU 158/1-1). All from type horizon; for localities see Table 1.

Diagnosis.—An asterolepidoid antiarch of small size, with length of the ventral wall of the trunk armour of about 75 mm, and with relatively high trunk armour. Paranuchal plate small, asymmetrical, slightly longer than it is wide. Ventral lateral ridge is well developed along the whole length of the trunk armour. The ventral wall of the trunk armour is flat. The contact face for mixilaterial plate on the anterior ventral lateral plate is short. Lateral margin of the ventral lamina of posterior ventral lateral plate almost straight. Length/width index of lateral lamina of posterior ventral lateral plate is about 2.3. Ornamentation generally consists of small tubercles sometimes fused into tuberculate ridges; tubercles tend to form rows perpendicular or parallel to the margins of the plates. The anterior ventral lateral plates bear a fine-meshed network of the shallow pits in the anterior part of the ventral lamina, and small tubercles with sharp tips along the margins in the posterior portion of the plate.

Description.—Only the Pn plate is known from the skull roof of Sherbonaspis talimaae sp. nov. This plate has not been described either in Sherbonaspis hillsi (Young and Gorter 1981) or in Sherbonaspis andreanna (Panteleyev 1993). The right Pn plate BNTU 44/1-13a (Fig. 3C) is subsquare in shape, with the maximum width in its posterior part. It is longer than broad, like in Pterichthyodes milleri (Miller, 1841) (Hemmings 1978: 16), with the B/L index of 0.88, in a sharp contrast to species of Asterolepis (e.g., Lyarskaya 1981) or Walterilepis speciosa (Gross, 1933) (Lukševičs 2021) with the B/L index of 1.12–1.34. The posterior margin of the bone is straight, with a narrow (short) and weakly developed smooth obtected nuchal area. The lateral segment of the bone is narrow, only 0.16 times as wide as the medial segment, in contrast to Walterilepis speciosa with the index of 0.35–0.49. The mpg is well seen and long almost reaching the medial margin (Fig. 4B) thus differing well from Byssacanthus dilatatus (Eichwald, 1844) (Karatajūtė-Talimaa 1960) and Walterilepis speciosa. The infraorbital sensory line canal on the head shield (ifc1) is well discernible in the posterior part of the lateral margin. The external surface shows a well-defined paramarginal crest (cr.pm) dividing the surface into two regions approximately equal in width. The posterolateral corner of the shallow oticooccipital depression is rounded. The external ornamentation consists of low small tubercles in places fused into radially arranged tuberculate ridges radiating from the posterior lateral angle of the plate.

Thorax: The left AVL plate BNTU 121/20-1 is partially preserved bone showing only the ventral lamina; almost all of the lateral lamina and processus brachialis are missing (Fig. 3A); this specimen is very thin, extremely fragile, and relatively small (only 41 mm in length). The right AVL plate
BNTU 44/2-1 is even less complete, comprising approximately half of the posterior part of both ventral and lateral laminae (Fig. 3B). Length of the ventral lamina in BNTU 44/2-1 is estimated at about 20 mm. All almost all edges of the ventral lamina of the AVL plate in BNTU 44/2-1 are well preserved, except the slightly damaged middle portion of the mesial edge. In contrast, most edges of the lateral lamina of the AVL in BNTU 121/20-1 are damaged, except the ventral lateral ridge and a narrow strip of bone along the ridge. The angle between the ventral and lateral laminae cannot be measured because the lateral lamina is almost absent in BNTU 121/20-1, and because both ventral and lateral laminae in BNTU 44/2-1 form too obtuse angle due to deformation of the specimen. In its squarish outline the ventral lamina resembles that of *Byssacanthus dilatatus* (Eichwald, 1844), *Stegolepis jugata*, *Sherbonaspis hillsi* Panteleyev, 1993, or *Stegolepis jugata* Malinovskaya, 1973 (Karatajūte-Talimaa 1960; Malinovskaya 1973; Young and Gorter 1981; Lukševičs 2021), and differs from species of *Asterolepis* (e.g., Lyarskaya 1981). It is moderately elongated with a B/L index of about 0.5, resembling that in *Sherbonaspis hillsi*, being larger than the index in *Stegolepis jugata* or *Walterilepis speciosa* (Malinovskaya 1973; Young and Gorter 1981; Lukševičs 2021). The ventral lamina is almost flat, as in *Byssacanthus dilatatus*, *Stegolepis jugata*, *Sherbonaspis hillsi*, and *Walterilepis speciosa* (Karatajūte-Talimaa 1960; Malinovskaya 1973; Young and Gorter 1981; Lukševičs 2021), and in contrast to *Gerdalepis rhenana* (Beyrich, 1877) and *Gerdalepis jesseni* Friman, 1982 (Gross 1941; Friman 1982) or *Wurungulepis Young, 1990* (Young 1990), where it is convex. The subcephalic division is relatively short and comprises about 21% of the length of the ventral lamina similarly as in *Sherbonaspis hillsi* (Young and Gorter 1981); the subcephalic division is rather short also in *Stegolepis jugata* (Malinovskaya 1973: 75). This division is only slightly shorter than the subcephalic division in *Walterilepis speciosa* (Lukševičs 2021) and significantly shorter than that in *Pterichthyodes milleri* (Miller, 1841 ex Agassiz MS) (Hemmings 1978: 30). The anterior margin is well preserved in BNTU 121/20-1, which shows a distinct anterolateral corner (c.al), as is the notch for the semilunar plate (Fig. 4A2; cf.Sm). The anterior margin of the AVL is rounded; it is formed of two almost equal parts: the anterior lateral part is almost straight forming about 135° wide angle with a rounded anterior mesial part of this margin. The right AVL overlies the left one similarly as in *Pterichthyodes milleri*, *Sherbonaspis hillsi*, and *Stegolepis jugata*, but in contrast to *Walterilepis* (Malinovskaya 1973; Hemmings 1978; Young and Gorter 1981; Lukševičs 2021).
The lateral margin is almost straight, it is only slightly convex in the anterior part. It is easy to discern that the mesial margin is subdivided into three portions for contact with the semilunar plate anteriorly (cf. Sm), with the opposite AVL plate in the middle (oa.AVL), and with the median ventral plate posteriorly (cf. MV). The shape of the notch for the semilunar plate (cf. Sm; Fig. 4A) suggests a narrow trapezoidal shape for this plate, and not a quadrilateral shape as in Stegolepis and Pterichthyodes (e.g., Malinovskaya 1973; Hemmings 1978) or in at least one AVL of Sherbonaspis hillsi (Young and Gorter 1981: fig. 18); the semilunar plate is about as long as it is wide. However, the semilunar plate remains unknown, hence it is unclear whether it is paired as in Pterichthyodes milleri or not. The contact area with the opposite AVL plate is rather strongly convex, it is about three times longer that the notch for the semilunar plate (cf. Sm), and about 1.8 times longer than the overlapping area of the MV plate (cf. MV). The area overlapping the median ventral plate is moderately wide. The area overlapping the PVL plate (cf. PVL) is rather long; the ventrolateral corner is rounded, but well discernible particularly on the visceral surface. The ventral division of the crista transversalis interna anterior (cit1) is rather low laterally, and decreases in height mesially. It is not subdivided mesially, similarly as in Sherbonaspis hillsi (Young and Gorter 1981: fig. 18), but in contrast to species of Asterolepis, Pterichthyodes, and Walterilepis (e.g., Hemmings 1978: 23; Lyarskaya 1981; Lukševič 2021). A low ridge stretches from the lateral end of the crista transversalis interna anterior to the anterolateral corner, similarly as in Sherbonaspis hillsi (Young and Gorter 1981: fig. 18A, C).

The lateral lamina is reconstructed at about 2.4–2.8 times as long as high, resembling proportions of the lateral lamina in Sherbonaspis hillsi and Stegolepis jugata (Malinovskaya 1973; Young and Gorter 1981), being proportionately higher than in Byssacanthisus dilatatus (Karatajutė-Talimaa 1960: pl. 3: 2), but significantly lower than in Wurungulepis denisoni and Walterilepis speciosa (Young 1990: fig. 12; Lukševič 2021: fig. 6). Judging from the outline of the dorsal margin in BNTU 44/2-1, it could be highest at the posterodorsal corner (pdc), similarly to Pterichthyodes milleri (Hemmings 1978: figs. 13, 14), Stegolepis jugata (Malinovskaya 1973: 77), and Sherbonaspis hillsi (Young and Gorter 1981: 106, fig. 18) but in contrast to Walterilepis speciosa (Lukševič 2021), where it is highest at the anterodorsal corner. The contact face for the MxL is shorter than in Byssacanthisus dilatatus, Pterichthyodes milleri, and Sherbonaspis hillsi. The shape of the foramen axillare (f.ax) is not known since it is not preserved in both available specimens.

The ornamentation is not well seen on the photographs of the specimen BNTU 121/20-1 due to glue covering the surface; however, it is well seen on the surface of the specimen. AVL plates are ornamented with a fine-meshed network of the shallow pits in the anterior part of the ventral lamina, and small tubercles with sharp tips along the margins in the posterior portion of the plate, which are well seen in BNTU 44/2-1 (Fig. 3), as well as in BNTU 121/20-1 under oblique lighting. In places these sharp small tubercles are fused by their bases in rows forming narrow ridges distributed al-

Fig. 5. Drawings of the left ventral lateral plates of the antiarch placoderm Sherbonaspis talimaae sp. nov.; upper Emsian of Belarus. A. BNTU 158/1-1 from Smol’ki 6п borehole, in lateral view. B. BNTU 44/2-2 from Osipovichi 6 borehole, in external view. Abbreviations: cf.MV, area overlapping the median ventral plate; cf.PVL, area overlapping the opposite PVL plate; dc, dorsal corner; oa.AVL, area overlapped by the anterior ventral lateral plate; pdc, posterior dorsal corner; vlr, ventral lateral ridge.

Fig. 6. Reconstruction of the ventral wall of the trunk armour of the antiarch placoderm Sherbonaspis talimaae sp. nov., based on BNTU 44/2-1, 44/2-2, 121/20-1, and 158/1-1; upper Emsian of Belarus. Abbreviations: AVL, anterior ventral lateral plate; MV, median ventral plate; MxL, mixilateral plate; PVL, posterior ventral lateral plate; Sm, semilunar plate.
most perpendicularly to the margins of the plate. The lateral lamina in specimen BNTU 44/2-1 shows similar ornamentation consisting of small tubercles.

Left PVL plate BNTU 44/2-2 is well preserved despite being flattened so that the angle between the ventral and lateral laminae appears very obtuse (Fig. 3D). Another left PVL plate BNTU 158/1-1 is less complete, particularly the ventral lamina is fairly damaged; however, the lateral lamina is well preserved (Fig. 3E). The PVL plate is rather small, reaching only 18.7 mm in length in the specimen BNTU 44/2-2 and about 30 mm in BNTU 158/1-1. Almost all edges of the ventral lamina of the PVL plate in BNTU 44/2-2 are well preserved, except the middle and posterior portion of the mesial edge, which are represented by the impression on the surface of the rock, and the anterior margin coinciding with the area overlapped by the AVL plate. In contrast, most edges of the ventral lamina in BNTU 158/1-1 are damaged. Almost all edges of the lateral lamina of the PVL are well preserved in both specimens, except small portion along the anterior dorsal margin in BNTU 158/1-1. The angle between the ventral and lateral laminae cannot be measured with confidence due to deformation of both specimens of the PVL plate; the measured angle is about 145° wide, which is too large to be undeformed. The ventral lamina is moderately elongated with a B/L index of about 0.44, resembling that as it is restored in *Sherbonaspis hillsi*, with the B/L index of 0.47 (Young and Gorter 1981: fig. 15), and being relatively longer than that in *Sherbonaspis andreanae*, with the B/L index of 0.4 (Panteleyev 1993: 66). The index is larger than the B/L index in *Stegolepis jugata* (Malinovskaya 1973: pl. 9: 6; B/L index of 0.4), and slightly smaller than that in *Pterichthyodes milleri* (Hemmings 1978: text-fig. 15; B/L index 0.47–0.52, 0.5 on the average). The subanal division is relatively short and comprises about 21% of the total length of the ventral lamina similarly as in *Sherbonaspis hillsi* (Young and Gorter 1981), which is less than the corresponding proportion in *Sherbonaspis andreanae* (Panteleyev 1993), *Stegolepis jugata*, and *Pterichthyodes milleri*. The lateral margin is almost straight, being gently convex in the anterior part; it bears small closely set prominent tubercles along the ventrolateral ridge and the whole lateral edge. The area overlapping the MV plate is rather long (Fig. 5B) indicating a relatively large MV plate (Fig. 6), as in *Stegolepis*, *Byssacanthus*, and *Sherbonaspis*, and in contrast to *Pterichthyodes* and *Gerda lepis* (Gross 1941; Karatajtė-Talimaa 1960; Malinovskaya 1973; Hemmings 1978; Young and Gorter 1981). The left PVL overlies the right one similarly as in species of *Pterichthyodes*, *Sherbonaspis*, and *Stegolepis*. The ventral lamina is about 1.5 times broad as the lateral lamina is high. The length/width index for the lateral lamina is 2.3 in BNTU 44/2-2, similarly as in *Byssacanthus dilatatus*, proportionally higher than in *Stegolepis jugata* or species of *Astrolepis*, but proportionally lower than in *Sherbonaspis hillsi*, *Wurungulepis denisoni* and *Gerda lepis jesseni* (Karatajtė-Talimaa 1960: pl. 3: 4; Malinovskaya 1973: pl. 9: 6; Young and Gorter 1981: 107; Friman 1987: fig. 5; Young 1990: fig. 12). The dorsal margin of the lateral lamina is almost straight anteriorly from the prominent dorsal corner (dc). The posterior margin of the lateral lamina is concave; overall shape of the lateral lamina resembles that in *Sherbonaspis hillsi* and *Sherbonaspis andreanae* (Young and Gorter 1981: fig. 15D; Panteleyev 1993: fig. 4a), but differs from that in *Pterichthyodes milleri*, *Byssacanthus dilatatus*, *Wurungulepis denisoni*, or *Stegolepis jugata*. The external surface of the posterior portion of the PVL plate BNTU 44/2-2 has been lost, but the slightly elevated area in the impression of the visceral surface indicates a broad transverse thickening on the ventral lamina. The PVL plates are ornamented with small tubercles sometimes fused into tuberculate ridges; tubercles tend to form rows usually perpendicular or in places parallel to the margins of the plate.

Remarks.—*Sherbonaspis talimaae* sp. nov. differs well from such asterolepidoids as *Wurungulepis denisoni*, *Byssacanthus dilatatus*, asterolepids, *Pterichthyodes milleri*, *Gerda lepis rhenana* and *Gerda lepis jesseni*, and Walterilepis speciosa by many features. *Sherbonaspis talimaae* sp. nov. resembles *Sherbonaspis hillsi* in (i) small size; (ii) B/L index of ventral lamina of AVL; (iii) short subcephalic division; (iv) semilunar plate which is as long as it is broad; (v) semilunar plate with a narrow trapezoidal shape; (vi) crista transversalis interna anterior (cit1) which is not subdivided mesially; (vii) proportions and shape of the lateral lamina of AVL; (viii) shape and proportions of the ventral lamina of PVL; (ix) short subanal division; (x) tubercular ornamentation. *Sherbonaspis talimaae* sp. nov. differs from *Sherbonaspis hillsi* in (i) that the lateral margin of the ventral lamina of PVL is almost straight; (ii) L/B index of lateral lamina of PVL. *Sherbonaspis andreanae* is a somewhat larger fish; however, it resembles *Sherbonaspis talimaae* sp. nov. in various features, but differs in: (i) B/L index of the ventral lamina of PVL; (ii) shorter subanal division; (iii) L/B index of lateral lamina of PVL; (iv) more ridged ornamentation. *Sherbonaspis talimaae* sp. nov. resembles *Stegolepis jugata* in (i) the short subcephalic division; (ii) proportions of the lateral lamina of AVL; (iii) tuberculate ornamentation. However, it differs from *Stegolepis jugata* in (i) B/L index of ventral lamina of AVL; (ii) shape and (iii) proportions of the semilunar plate; (iv) L/B index of lateral lamina of PVL; (v) less ridged ornamentation.

Stratigraphic and geographic range.—Upper Emsian/lower Eifelian, Lower/Middle Devonian; eastern part of Belarus.

Discussion

Taxonomic remarks.—The Antiarcha is currently considered as the most basal group of jawed vertebrates (Brazeau 2009; Zhu et al. 2012, 2013; Pan et al. 2017) comprising yunnanolepids, *Minicrania*, sinolepids and euantiarchs (Zhu 1996; Zhu and Janvier 1996). Euantiarchs, consisting of two suborders, the Bothriolepidoidei and the Astrolepidoidei,
are defined by the well-developed brachial process (Young and Gorter 1981; Janvier and Pan 1982; Zhu 1996; Zhu and Janvier 1996; Lukševičius 2001). However, some authors treat these two groups as the orders Bothriolepiformes and Asterolepiformes (Moloshnikov 2010, 2012; Van der Laan 2018). At least six families were established within the Asterolepidoidea: Asterolepididae Traquair, 1888, Remigolepididae Stensiö, 1931, Pterichthyodidae Stensiö, 1948, Lepadolepididae Berg, 1955, Pambulaspidae Young, 2010, and Asperaspidae Moloshnikov, 2012.

Young and Gorter (1981) originally attributed the genus Sherbonaspis to the family Pterichthyidae. They also provided a shortened definition of the Pterichthyidae from the diagnosis proposed by Hemmings (1978) and attributed Stegolepis to this family, following Malinovskaya (1973). Later Panteleyev (1993) followed this attribution establishing another species of Sherbonaspis, namely Sherbonaspis andreae. Previously Karatajute-Talina (1960, 1963) and Obручев (1964) had included Pterichthyodes, Byssacanthus, and Gerdalepis in the family Pterichthyidae. Berg (1955) established a separate family Lepadolepididae containing Gerdalepis, Grossaspis, and Lepadolepis, whilst Gross (1965) suggested to unite Gerdalepis, Grossaspis, and Lepadolepis into a subfamily Gerdalepidinae within the Pterichthyidae. Zhu (1996) provided a cladistic analysis of all antiarchs and demonstrated that the Pterichthyidae as defined earlier appears polyphyletic. The most comprehensive recent analysis of antiarch relationships based on 42 ingroup taxa and 50% majority-rule consensus trees show a polytomy consisting of five genera (Wurungulepis, Byssacanthus, Stegolepis, Pterichthyodes, and Sherbonaspis) and two sister-groups, Asterolepididae and Lepadolepididae of some authors, thus demonstrating Pterichthyidae as a polyphyletic group. However, some taxa of antiarchs described before 2018 were not included in the analysis of Wang and Zhu (2018), e.g., Asperaspis carinata Panteleyev, 1993, from the Givetian of Kazakhstan, and Merimbulaspis meemaneae Young, 2010, from the ?Givetian/Frasnian of New South Wales, Australia.

Moloshnikov (2012) attributed Asperaspis to a separate family Asperaspidae containing only one genus and thus being a redundant taxonomic unit. Asperaspis differs well from other asterolepidoid antiarchs in the absence of the median ventral plate of the trunk armour, and in short subcaudal region of the ventral wall of trunk shield. It differs from Asterolepis in the well-developed separate PDL plate and PL plate, as well as in the unpaired semilunar plate. It differs also from Remigolepis in the unpaired semilunar plate. However, Asperaspis demonstrates the low, relatively long trunk armour, thus more closely resembling Asterolepis and Remigolepis, and not pterichthyodids or lepadolepidids with generally short and high trunk armour.

Young (2010) described Merimbulaspis from a small collection of plates with distinctive ornamentation, separate PDL plate, similar overlap relationships between the dorso-lateral plates of the trunk armour and the location of the lateral line sensory groove on a separate PL plate, thus indicating a close relation to Pambulaspis. These similarities were used to erect a separate family Pambulaspidae (Young 2010).

Despite the polyphyletic condition having been demonstrated for the family Pterichthyidae, some authors continue using this grouping. Moloshnikov (2012) attributed Sherbonaspis to the family Pterichthyidae, some authors continue using this grouping. Moloshnikov (2012) attributed Sherbonaspis to the family Pterichthyidae, some authors continue using this grouping. Moloshnikov (2012) attributed Sherbonaspis to the family Pterichthyidae, some authors continue using this grouping. Moloshnikov (2012) attributed Sherbonaspis to the family Pterichthyidae, some authors continue using this grouping.
Fig. 7. Phylogeny of 45 taxa of Antiarcha. A. Strict consensus tree of 185 most parsimonious trees based on the data-set from Wang and Zhu (2018), with addition of one character (SOM: character 80) and three antiarchs species (Asperaspis carinata, Walterilepis speciosa and Merimbulaspis meemannae). B. 50% majority-rule consensus tree of the 185 most parsimonious trees. Numbers on branches indicate the percentage of most parsimonious trees that contain a particular clade. Legend: B, taxa traditionally attributed to Bothriolepidoidea. Taxa in bold traditionally attributed to Asterolepidoida.
arate Bothriolepidoidei and Asterolepidoidei (Fig. 7). For instance, *Ningxialepis* from the Famennian of China and *Kirgisolepis* from the Upper Devonian of Kyrgyzstan are shown as the sister group of *Byssacanthus* from the Eifelian/Givetian of the Baltic Devonian Basin, most probably due to the dorsal spine on the AMD plate. However, the dorsal spine in *Byssacanthus* is situated almost in the middle of the AMD plate (Karatajūte-Talimaa 1960), whereas in *Ningxialepis* and *Kirgisolepis* it appears on both the AMD and PMD plates (Jia et al. 2010; Panteleyev 1992). In most previous analyses *Ningxialepis* and *Kirgisolepis* were attributed to Bothriolepidoidei, being closely related to *Jiangxilepis* (Jia et al. 2010; Moloshnikov 2012). Moloshnikov (2012) has attributed *Kirgisolepis* along with *Dianolepis*, *Jiangxilepis*, and *Ningxialepis* to the family Dianolepididae, subfamily Dianolepidinae.

The strict consensus tree of all antiarch taxa shows that *Asperaspis* might be attributed to the family Asterolepididae, or it is a sister taxon of the Asterolepididae + Pambulaspidae in accordance with the 50% majority-rule consensus tree. The other family-level groups are the Pambulaspidae and Lepadolepididae. All the other Asterolepidoidei are forming a wide group of relatively small fishes including *Byssacanthus*, *Hunanolepis*, *Pterichthyodes*, *Sherbonaspis*, *Stegolepis*, *Walterilepis*, and *Wurungulepis*. The 50% majority-rule consensus tree, however, allow to separate two groups of asterolepidooids. One group consists of *Byssacanthus*, *Wurungulepis*, *Hunanolepis*, and two more crown-ward placed clades. The
first contains *Pterichthyodes*, *Ningxialepis*, and *Kirgisolepis*, and the second *Sherbonaspis* and *Walterilepis*, which are more closely related to Lepadolepididae. The second group contains *Stegolepis*, *Asperaspis*, and *Asterolepididae + Pambulaspidae*.

However, the cladistics analysis of Euantiarcha alone (31 ingroup taxa) demonstrates a slightly different situation (Fig. 8). Both the strict consensus tree and the 50% majority-rule tree calculated from the 124 best trees shows relatively stable cladogram and clear distinction of Bothriolepidoidei (including *Ningxialepis* and *Kirgisolepis*, which appear as a sister group of *Jiangxilepis*) and Asterolepidoidei with *Hunanolepis* as one of the basal-most asterolepidoids. In accordance with the strict consensus tree and the 50% majority-rule tree *Sherbonaspis* is closely related to *Pterichthyodes*, *Wurungulepis*, and *Walterilepis*, as well as to the Lepadolepididae. Two genera, *Stegolepis* and *Byssacanthus*, form a small clade situated between the *Asperaspis + Asterolepididae + Pambulaspidae*, and all the other small asterolepidoids. Bootstrap values indicate strong support (79) for monophyly of Pambulaspidae, moderately strong support (62) for a monophyly of *Ningxialepis* and *Kirgisolepis*, the same value of support (62) for Lepadolepididae. Moderately strong support (50) suggests close relationships of Pambulaspidae with *Asterolepis* and *Remigolepis*. The other grouping all are weakly supported. However, these results demonstrate that the phylogenetic analysis of the Euantiarcha alone provides more reliable results if compare with the analysis of all antiarchs together. This is presumably because the number of characters that are uncodable for some taxa increases in case of all antiarchs, therefore certain homology judgements become less reliable. These results also clearly support the point of view of Young (2010) that there are too many gaps in our knowledge of antiarch morphology, therefore any phylogenetic scheme still should be treated as very tentative.

**Palaeogeography and stratigraphic record.**—Antiarchs are among the most widely distributed placoderm fishes of the middle Palaeozoic (e.g., Zhao and Zhu 2010; Dupret et al. 2023), particularly such genera as *Bothriolepis* and *Remigolepis*. However, several groups of antiarchs show a high degree of endemism. Members of Asterolepidoidei (including poorly known species of *Venezuelepis*) have hitherto been reported from Antarctica, Australia, Central Asia (Kazakhstan and Kirgisia), China, Euramerica, and South America (e.g., Young and Moody 2002; Zhao and Zhu 2010; Moloshnikov 2012). The most ancient asterolepidoids occur in the Emsian from the Georgina Basin in Central Australia (Young 1984), where a small possibly juvenile asterolepidoid slightly resembling *Pterichthyodes* was found, and the Emsian/Eifelian of New South Wales, Australia, producing *Sherbonaspis hillsi* (Fig. 9). The age of the fossil bearing deposits of *Sherbonaspis hillsi* originally was reported as the early Eifelian (Young and Gorter 1981), but later was re-evaluated as probably late Emsian or earliest Eifelian (Hunt and Young 2012). Another early asterolepidoid, *Wurungulepis denisoni* Young, 1990, is known from the Eifelian of Queensland, Australia (Young 1990). Two more species of *Sherbonaspis*, namely *Sherbonaspis andreannae* has been recorded in the Givetian of Kazakhstan (Panteleyev 1993), and *Sherbonaspis talimaae* sp. nov. in the “upper Emsian of Belarus. Prior to this study, the oldest asterolepidoids from Euramerica were *Byssacanthus* from Eifelian–Givetian of the Baltic Devonian Basin, an unnamed antiarch probably related to *Byssacanthus* and *Gerdalepis* (Otto 1999), and *Gerdalepis jesseni* Friman, 1982, from the middle Eifelian of Germany. *Pterichthyodes milleri* comes from Eifelian–lower Givetian of Scotland (Hemmings 1978). The known evidence suggests that asterolepidoids were apparently absent in the Early Devonian of China. Instead, the earliest members of asterolepidoid group occur in Gondwana, and appear slightly later in Belarus, later almost simultaneously elsewhere on the territory of the East European Platform, in Germany, China, and Kazakhstan. This agrees with the suggestion of Young (1984; see also Young et al. 2010) that the primary distribution of asterolepidoid antiarchs did not include South China and consideration that asterolepidoids originated elsewhere but not in South China. However, it is difficult to decipher the dispersion routes of early asterolepidoids, particularly taking into account the small size and possible swimming abilities of these bottom-dwelling fishes.

All the other species of asterolepidoid antiarchs are recorded in the younger strata, from the Givetian up to the Famennian (Fig. 9). Some of these antiarchs show almost
cosmopolitan distribution, e.g., several species of *Remigolepis* are known from Australia, Belgium, China, Central Russia, East Greenland, and Kazakhstan, as well as possible *Remigolepis* reported from Scotland (Andrews 1978; Johanson 1997; Lukševičs 1991; Olive 2015; Pan et al. 1987; Panteleyev 1992).

Stratigraphy.—All of the material of *Sherbonaspis talimaae* sp. nov. described above comes from the deposits of the upper part of the Vitebsk Formation, corresponding to the Lepel Beds, Vitebsk RS. In accordance with the current Devonian stratigraphical chart of Belarus (Obukhovskaya et al. 2010) the Vitebsk RS corresponds to the upper Emsian. Rocks of the Lepel Beds usually overlap deposits of the Obol Beds of the same Vitebsk RS or lie on the Precambrian basement. Lepel Beds are covered everywhere with deposits of the Adrov RS corresponding to the Middle Devonian Eifelian Stage. The Lepel Beds contain various ostracods, lingulate brachiopods, and a rich assemblage of fishes including acanthodians, placoderms and other fishes from the *Laliacanthus singularis* Acanthodian Zone and the *Skamolepis fragilis* Thelodont Zone (Mark-Kurik 2000; Valiukevičius and Kruchek 2000). As it already mentioned above, deposits of the Lepel Beds correspond to the *Diaphanospora inassueta* Miospore Zone (Valiukevičius and Kruchek 2000), or the upper part of the *Rhabdosporites mirus–Gneudnaspora divellomedium* Miospore Zone, while in terms of conodonts they roughly correspond to the upper part of the *Polygnathus costatus patulus* Zone of the previous version of conodont zonation (Obukhovskaya et al. 2010). However, conodonts have not been found in the deposits of the Vitebsk Formation. Recently Vodrážková et al. (2011) granted *Polygnathus patulus* and *P. partitus* full species status. Hence, the Upper *Polygnathus patulus* Zone (now *Polygnathus partitus* Zone) subsequently defines the Emsian/Eifelian boundary: *Polygnathus patulus* Zone corresponds to the uppermost Emsian and *Polygnathus partitus* Zone corresponds to the lowermost Eifelian in a modern conodont zonation (e.g., Aboussalam et al. 2015). In the Baltic States, almost all the authors have treated the upper part of the Rēzekne Formation as the approximate age analogue of the deposits of Lepel Beds of Belarus (Lyarskaya 1978; Lyarskaya and Kleesment 1981; Mark-Kurik 2000; Valiukevičius and Kruchek 2000; Obukhovskaya et al. 2010). However, the Emsian/Eifelian boundary in the Baltic States still is a matter of discussion (Fig. 10). The *Laliacanthus singularis* Acanthodian Zone is common for both the Rēzekne and Pārnu formations; this zone supposedly marks the beginning of a Middle Devonian level in acanthodian phylogenetical development (Valiukevičius and Kruchek 2000). From another aspect, the age of the *Laliacanthus singularis* Zone is different in accordance with the acanthodian and miospore zonation. According to miospores, the lower part of the Rēzekne Formation is late Emsian in age, whereas the upper two members of the Rēzekne Formation correspond to the Periplecotriletes tortus Zone and are dated as earliest Eifelian (Valiukevičius and Kruchek 2000). Attribution of the Rēzekne Formation to the upper Emsian by Mark-Kurik (e.g., Mark-Kurik 2000; Mark-Kurik and Põldvere 2012) is based on the distribution of placoderms *Wijdeaspis* and the *Skamolepis fragilis* Thelodont Zone. However, acanthodians found together with *Wijdeaspis* correspond to an older assemblage than that of the *Laliacanthus singularis* Zone (Valiukevičius and Kruchek 2000). It seems that the data on miospore distribution and their correlation to the conodont zones remain controversial. Thus, Mark-Kurik (2000: 312) stated that “it is reasonable for the time being to preserve the boundary in the Baltic between the Rēzekne and Pārnu formations”. However, analysis of distribution of various vertebrates in the Middle Devonian of the East European Platform (Lukševičs et al. 2010) supported the view of Valiukevičius and Kruchek (2000) that the *Laliacanthus singularis* Zone might correspond in part to the upper Emsian, and in part to the lower Eifelian. Thus, the lower part of the Rēzekne Formation would correspond to the upper Emsian, and the two upper members to the lower Eifelian, with the upper part of the Rēzekne Formation in the modern stratigraphic scheme of Latvia corresponding to the lowermost Eifelian (Lukševičs et al. 2010; Lukševičs and Stinkulis 2018). If the correlation of the Lepel Beds with the upper part of the Rēzekne Formation is correct, then an early Eifelian age for *Sherbonaspis talimaae* sp. nov. cannot be excluded.
Conclusions

The new antiarch from the Vitebsk Formation, Lepel Beds, *Sherbonaspis talimaee* sp. nov., is based on the specimens collected from three boreholes in the central and eastern parts of Belarus. This new species shows independent PVL and PL plates, which constitutes one of apomorphic characters of Asterolepidoidei (Wang and Zhu 2018). *Sherbonaspis talimaee* sp. nov. resembles *Sherbonaspis hillaee* in the shape and proportions of the AVL and PVL plates, the shape of the notch for semilunar plate, and the character of ornamentation. The result of a new cladistic analysis of the Euantiarcha supports the traditional subdivision of the group into Bothriolepidoidei and Asterolepidoidei; however, polyphyly of Pterichthyidae is in agreement with the hypothesis of Zhu (1996). Until the phylogenetic relationships of Asterolepidoidei are better resolved, *Sherbonaspis* is attributed to Pterichthyidae. The comparison of the sections of the Lepel Beds of Belarus with the age-equivalent deposits from Estonia and Latvia shows the necessity of further stratigraphic studies including such age-markers as conodonts and spores to clarify a late Emsian or possibly of further stratigraphic studies including such age-markers as conodonts and spores to clarify a late Emsian or possibly early Eifelian age for the Lepel Beds. The new antiarch taxon is a significant taxonomic addition to the Emsian/Eifelian fish assemblage from the western part of the East European Platform.

Authors’ contributions

D. Plax, investigation, visualization, writing: original draft; E. Lukševičs, formal analysis, software, visualization, writing: review and editing.

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