Revision of asterolepidoid antiarch remains from the Ogre Formation (Upper Devonian) of Latvia

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Abstract. The Frasnian (Upper Devonian) antiarch *Walterilepis speciosa* was first described in 1933 (as *Taeniolepis*) on the basis of a single specimen. The newly collected material has allowed the head to be described in a more detail, especially the nuchal and paranuchal plates. Other newly described elements include bones of the pectoral appendages and trunk armour, demonstrating a rather high and short trunk armour. The shape and proportions of the head and trunk armour suggest the attribution of *Walterilepis* to the family Pterichthyodidae; it is most probably closely related to *Lepadolepis* from the Late Frasnian of Germany. Whilst *W. speciosa* is endemic to the Latvian part of the Baltic Devonian Basin, the connection to the Rheinisches Schiefergebirge is probably closer than previously presumed. *Walterilepis* fits into the biostratigraphical column at the same level as *Bothriolepis maxima* and *B. evaldi*, indicating the high diversity of antiarchs during Pamūšis time.

Key words: Frasnian, biostratigraphy, morphology, placoderm, Baltic Devonian basin.

INTRODUCTION

The well-known Baltic German palaeontologist Walter Gross, who was born in the close vicinity of Riga, made a great contribution to research on Devonian vertebrates of Estonia and Latvia. He collected fossil fishes in Latvia in the 1930s with his brother, local collector Roland Gross, and Dr Nikolajs Delle from the University of Latvia (Gross 1933a). It is not clearly stated who collected a single specimen (Museum für Naturkunde Berlin No. MB f 136), consisting of articulated nuchal and postpineal plates, at the left bank of the Daugava River close to the former Bramberģe manor house (*Brambergshof* in German: Gross 1933a; fig. 1; locality C, Fig. 1A). The specimen without description was first named by Gross *Taeniolepis speciosa* in his catalogue of antiarchs (1932) and the description was published a year later (Gross 1933a). He determined that it was a new genus and species of antiarchan fish, differing from both *Asterolepis* and *Bothriolepis* in characteristic ornamentation consisting of smooth, radially arranged ridges. Later Gross (1942) provided details of the stratigraphic level for the specimen; it came from the e/f beds (*e/f Stufe* in German: Gross 1942, p. 400), corresponding to the lower part of the Ogre Formation, upper part of the Frasnian, in the modern stratigraphic chart of Latvia. Moloshnikov (2001) noted that the generic name of Gross (1932, 1933a) is preoccupied by the sarcopterygian name *Taeniolepis* Trautschold, 1874, and he erected the replacement name *Walterilepis* (Moloshnikov 2001). Following Denison (1978), Moloshnikov erroneously gave 1932 as the year of description, but this is a *nomen nudum*; the description of this taxon was not published until 1933. Recently a new material of *Walterilepis* has been collected from Eastern Latvia enabling the revision of this taxon. The main aim of this article is to revise all asterolepidoid material from the Ogre Formation, to provide a more accurate description of the species *Walterilepis speciosa* and to establish its systematic position within antiarchs.

GEOLOGICAL SETTING

The Upper Devonian is the most complete and widely exposed part of the Devonian section in Latvia where both the Frasnian and Famennian stages are present. The lithostratigraphy of this sequence in Latvia is rather well established (Sorokin 1981a): the Frasnian section consists of the Amata(?), Pļaviņas, Salaspils, Dubnik (a lateral equivalent of the Salaspils Formation), Daugava, Katleši, Ogre, Stipinai and Amula formations (Fig. 2).

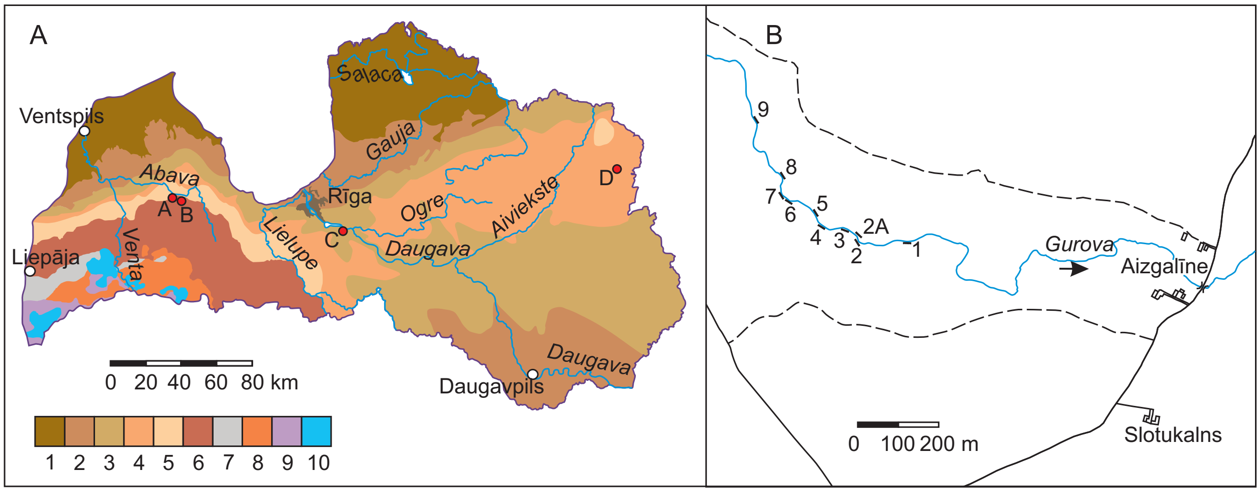

Fig. 1. A, generalized geological map of Latvia with fossil fish sites (circles designated by letters) where *Walterilepis speciosa* was collected; **B**, a sketch map showing the position of outcrops of the Ogre Formation along the Gurova River. A, modified from Stinkule & Stinkulis (2013, fig. 3). Legend for part A: 1, Middle Devonian Narva, Aruküla and Burtnieki formations; 2, Middle–Upper Devonian Gauja, Sietiņi, Lode and Amata formations; 3–6, Upper Devonian; 3, interval of the Pļaviņas–Daugava formations; 4, Ogre Formation; 5, Stipinai and Amula formations; 6, deposits of the Famennian Stage; 7, Carboniferous; 8, Permian; 9, Triassic; 10, Middle–Upper Jurassic. Fossil localities: A, Langsēde site along the Imula River; B, Kalnamuiža Mill site along the Amula River; C, Bramberģe site along the Daugava River (type locality); D, localities along the Gurova River. Numbers in part B designate the outcrops of the Ogre Formation along the Gurova River.

Conodont zones	Regional stages	Formations	Members	Placoderm and psammosteid zones
linguiformis	Amula	Amula		
rhenana	Stipinai	Stipinai	Bauska	
			Imula	
	Pamūšis	Ogre	Suntaži	*Bothriolepis maxima - Placosteus undulata*
			● Rembate	
			Lielvārde	
	Katleši	Katleši	Kuprava	
			Liepna	
			Ikšķile	
	Daugava	Daugava	Kranciems	*Bothriolepis traudscholdi - Psammosteus megalopteryx*
			Selgas	
jamieae			Oliņkalns	
hassi	Dubnik	Salaspils		
	Pļaviņas	Pļaviņas	Ape	
punctata			Atzele	
transitans			Sēlija	*B. cellulosa*
			Koknese	
falsiovalis	Amata	Amata		*B. prima - B. obrutschewi*
disparilis	Gauja	Gauja/Lode		*Ast. ornata - Ps. paradoxa*

Fig. 2. Stratigraphic chart of the uppermost Givetian–Frasnian deposits of Latvia. Modified from Stinkulis (2004), Lukševičs et al. (2012) and Lukševičs & Stinkulis (2018). Black point designates the stratigraphic level of this study.

Carbonate sedimentation dominated during the about 7.5-Myr-long time span of the Frasnian, while the territory was covered by a shallow epicontinental, sometimes restricted basin with changing salinity. The carbonate sedimentation was predominant in the interval of the Pļaviņas–Daugava regional stages and in the Stipinai Regional Stage. Several comparatively short episodes of clastic sedimentation occurred during the Frasnian, and the deposits of the Ogre Formation represent the results of one of such events. The Ogre Formation is composed of the sandstone, siltstone, dolomitic marl, sandy dolomite and rarely dolomite sandstone, clay and gypsum, overlying the eroded surface of the Katleši Formation, but in the northwestern and northeastern parts of Latvia in places it disconformably covers the Daugava Formation (Lukševičs et al. 2011).

The Ogre Formation consists of a 15–18 m (western Latvia) up to 50-m-thick (eastern Latvia) mainly siliciclastic sequence, composed of three members: the Lielvārde Member at the base, the Rembate Member in the middle and the uppermost Suntaži Member. The Lielvārde Member consists of sandstone, clay, dolomitic marl, siltstone, dolomite and gypsum-rich dolomite. Fish remains often form clusters, the so-called 'fish breccia' (Sorokin 1978). The middle part of the Ogre Formation, the Rembate Member, is composed of cross-stratified feldspar-quartz sandstone with a high mica content and carbonate cement, rhythmically alternating with argillite (clay), siltstone and dolomitic marl in eastern Latvia. The sandstone is found at the base of the rhythms. In the study area, in the Gurova Ravine, the Rembate Member is represented mainly by sandstone containing vertebrate fossils. The Suntaži Member comprises clay and dolomitic marl with siltstone and sandstone interbeds; most probably this member is missing in the study area.

The vertebrate assemblage of the Ogre Formation corresponds to the *Psammosteus falcatus* (now the zonal taxon is known as *Traquairosteus*? *falcatus*: Glinskiy 2018) and *Bothriolepis maxima* biozones, which correlate with the late *rhenana* Standard Conodont Biozone (Esin et al. 2000); conchostracans and lingulid brachiopods, although rare, have also been found in this formation (Sorokin 1981b). The vertebrate assemblage from the Ogre Formation in Latvia yields the heterostracomorphs *Traquairosteus*? *falcatus* (Gross) and *Psammosteus* sp., acanthodians *Devononchus laevis* Gross and Acanthodii gen. et sp. indet., porolepiform *Holoptychius* cf. *nobilissimus* Agassiz, dipnoans '*Dipterus*' cf. *marginalis* Agassiz and Dipteriformes gen. et sp. indet., osteolepiform *Platycephalichthys bischoffi* Vorobyeva and tetrapod *Obruchevichthys gracilis* Vorobyeva (Lukševičs et al. 2011). Besides these taxa, *Psammosteus tenuis* Obruchev, *Obruchevia heckeri* (Obruchev) and *Webererpeton sondalensis* Clément & Lebedev have been reported from the time-equivalent deposits of northwestern Russia (Esin et al. 2000; Clément & Lebedev 2014).

The Ogre Formation is well exposed in many outcrops along the Daugava, Ogre, Pededze and Tirza rivers in central and eastern Latvia (mostly Vidzeme), the Lielupe, Mūsa and Tērvete rivers in southern Latvia (Zemgale) and the Abava, Amula, Imula and Venta rivers in western Latvia (Kurzeme), as well as some other rivers. Fish remains from these various localities have been collected by several authors (Gross 1933a, 1942; Lyarskaya 1986; Lukševičs 2001; Lukševičs et al. 2011). However, no new specimens of *Walterilepis speciosa* were reported until 2017, despite extensive collection efforts. Thus, most researchers have treated *Walterilepis* as *incertae sedis* among Antiarcha (e.g. Denison 1978; Lyarskaya 1981), or *Familia incertae sedis* among Asterolepiformes (Karatajūtė-Talimaa 1963; Gross 1965), or among Asterolepidoidei (Moloshnikov 2008). Yet, two additional specimens of small antiarch fishes have been described from the same stratigraphic level of the Ogre Formation where *Walterilepis* comes from: one is Antiarchi gen. indet. from the Langsēde locality along the Imula River (Gross 1942), and the other is *Asterolepis*? *amulensis* Lyarskaya, 1981 from the sandstone deposits outcropping along the Amula River 500 m downstream from the Kalnamuiža watermill (Lyarskaya 1981). In the description of the latter Lyarskaya (1981) noted that the attribution of a single anterior ventral lateral (AVL) plate to the genus *Asterolepis* is conditional based only on several features resembling those of *Asterolepis syasiensis*, *Byssacanthus* and *Stegolepis*. Two additional specimens provisionally attributed to *Asterolepis*? *amulensis* were found by the author of this paper during the preparation of the material collected in 1981 at the Langsēde locality (Lukševičs et al. 2011). Considering that three bothriolepid species, namely *Bothriolepis maxima* Gross, 1933, *B. evaldi* Lyarskaya, 1986 and *Grossilepis spinosa* (Gross, 1942), have previously been described from the Ogre Formation (Lukševičs 2001), the total number of antiarch taxa from this formation is unusually high and needs to be revised.

That was the situation until the author together with the team of students and the graduates from the University of Latvia collected fish remains from a new locality of the Devonian fish remains and identified some new specimens of *Walterilepis speciosa*. The new material comes from several small outcrops along the Gurova creek in the picturesque Gurova Ravine in eastern Latvia (Stinkulis et al. 2020). This material includes plates that Gross (1933a) did not have available to study, such as an anterior median dorsal plate, a posterior median dorsal plate, an anterior ventrolateral plate, a central dorsal plate of the pectoral fin armour, a lateral plate and a paranuchal plate. Thus, a more accurate description of the species *Walterilepis speciosa* became possible. The detailed comparison with the other asterolepidoid antiarch species allowed the attribution of this species to the family Pterichthyodidae.

MATERIAL AND METHODS

The Gurova Ravine in eastern Latvia is in the vicinity of Aizgalīne village, Medņeva Parish, Viļaka municipality. Nine outcrops of the Upper Devonian, Frasnian Ogre Formation lie at a distance of 600 m on both banks of the Gurova River in the interval from about 1.5 km to approximately 2.1 km upstream from its confluence with the Kira River (Fig. 1). The detailed geological sections of four outcrops of the Ogre Formation from the Gurova Ravine were compiled by Ģirts Stinkulis, Simona Mačute, Terēze Reķe and the author of this article in 2017 and 2019. Five outcrops of sandstone, of the total of nine exposures, yield vertebrate remains at the Gurova site; the remains of *Walterilepis* have been found in all of them, namely in outcrops Nos 1, 5, 6, 7 and 8. The vertebrate remains (about 700 specimens identified to the specific or generic level) were collected by the participants in the Summer school in field palaeontology in 2017 and mechanically prepared by the author and T. Reķe using an optical microscope and a mounted needle. Most of the fish material occurs in the light grey, yellowish and light red sandstone, generally as disarticulated and fragmented plates, scales and spines. The bone tissue of *Walterilepis* is usually well preserved, brown or dark brown and shows little or no sign of abrasion by the current. Plates were measured with a digital Vernier calliper, studied under optical zoom in the binocular microscope Stemi 508 with the built-in photocamera Axiocam 208 Color and photographed with a Sony DSC-HX350 digital camera. Photogrammetry of the nuchal plate LDM Pl 10/523, paranuchal plate LDM Pl 10/524 and a partial lateral plate LDM Pl 10/526 was performed by Jurijs Ješkins; several hundreds of photos have been used to produce the 3D images of these bones. Digital models of the plates were exported into the modelling programme Blender 2.74 and used to produce the 3D reconstruction of a partial head shield. The studied material from the Gurova Ravine is kept in the Latvian National Museum of Natural History (LDM), Riga; collection No. LDM Pl 10.

Two specimens previously attributed to *Asterolepis*? *amulensis* are referred below to *Walterilepis speciosa*. These specimens come from the Langsēde locality, which has been previously described in detail (Lukševičs et al. 2011). These specimens are also kept in the LDM, collection No. LDM G 99. A partial and damaged anterior median dorsal plate from the same Langsēde locality, described by Gross (Langserde in Gross 1942) and kept in the Natural History Museum in Stockholm, is also referred to *Walterilepis*.

Institutional abbreviations. LDM, Latvian National Museum of Natural History, Riga, Latvia; MB, Natural History Museum (Museum für Naturkunde), Berlin, Germany; NRM, Natural History Museum (Naturhistoriska riksmuseet), Stockholm, Sweden.

Anatomical abbreviations. The following abbreviations are used in the text: adc, anterodorsal corner of AVL; ADL, anterior dorsal lateral plate; alr, anterolateral ridge; AMD, anterior median dorsal plate; AVL, anterior ventral lateral plate; Cd_1, dorsal central plate 1; Cd_2, dorsal central plate 2; cf.ADL, area overlapping the anterior dorsal lateral plate; cf.AMD, area overlapping the anterior median dorsal plate; cf.MxL, area overlapping the mixilateral plate; cf.PVL, area overlapping the posterior ventral lateral plate; cit_1, the anterior branch of the anterior transverse internal crest; cit_2, the posterior branch of the anterior transverse internal crest; cr.d, dorsal crest; cr.dm, dorsomesial crista; cr.pm, paramarginal crest; cr.pto, postorbital crest; cr.tp, transverse posterior internal crest; $d.end_1$, internal openings of the endolymphatic ducts; $d.end_2$, external openings of the endolymphatic ducts; f.ar, articular facet; f.artd, dorsal crest of the articular facet; f.ax, axillary foramen; $f.ax_1$, axillary foramen on the visceral surface; fmp, protractor area of processus brachialis; f.retr, levator fossa; l, lateral corner of AMD; La, lateral plate; Ml_2, lateral marginal plate 2; Mm_1, mesial marginal plate 1; Mm_2, mesial marginal plate 2; moc, median occipital crista; mpg, middle pit-line groove; MxL, mixilateral plate; Nu, nuchal plate; pbr, brachial process; p.co, pars condyloidea; pma, posterior marginal area; PMD, posterior median dorsal plate; Pn, paranuchal plate; Pp, postpineal plate; p.pe, pars pedalis of processus brachialis; pr, ventral process on the PMD; pt, ventral funnel pit; sna, supranuchal area; sol, suborbital lamina; sot, supraoptic thickening; vlc, ventrolateral corner of AVL; vlr, ventrolateral ridge.

SYSTEMATIC PALAEONTOLOGY

Suborder ASTEROLEPIDOIDEI Miles, 1968
Family PTERICHTHYODIDAE Stensiö, 1948

Definition (from Young & Gorter 1981). Asterolepidoids with a high and short trunk shield, the component plates being broad in proportion to their length. Distal segment of pectoral fin with two dorsal central and two ventral central plates.

Genus *Walterilepis* Moloshnikov, 2001

Type species. Walterilepis speciosa (Gross, 1933).

Diagnosis. As for the type species (by monotypy).

Walterilepis speciosa (Gross, 1933)
Figures 3–6

1932 *Taeniolepis speciosa* sp. nov.; Gross, p. 35 (*nomen nudum*).
1933a *Taeniolepis speciosa* n. g. n. sp.; Gross, p. 43, abb. 24, taf. IV, fig. 11.
1942 Antiarchi gen. indet.; Gross, pp. 422–423, abb. 12.
1964 *Taeniolepis speciosa* Gross; Obruchev, pl. VI, fig. 9.
1965 *Taeniolepis speciosa*; Gross, abb. 3G.
1981 *Asterolepis*? *amulensis* Lyarskaja, pp. 137–138, fig. 104; pl. XXXVII, fig. 5.
2001 *Walterilepis speciosa* (Gross); Moloshnikov, p. 214.
2011 *Asterolepis*? *amulensis* Lyarskaja; Lukševičs et al., p. 362.

Material and localities. Holotype: Museum für Naturkunde Berlin, No. MB f 136 (originally referred to without the number in Gross (1933a)), articulated nuchal and postpineal plates in dorsal view. Material from the Gurova Ravine, Latgale, eastern Latvia: LDM Pl 10/518–10/523, six nuchal plates; LDM Pl 10/524 and 10/525, paranuchal plates; LDM Pl 10/526, an incomplete left lateral plate; LDM Pl 10/527 and 10/533, fragmentary anterior median dorsal plates; LDM Pl 10/528 and 10/529, partial posterior median dorsal plates; LDM Pl 10/534, an incomplete, badly preserved trunk armour plate, possibly mixilateral plate; LDM Pl 10/530, the proximal part of the right central dorsal plate 1 of the pectoral fin, and LDM Pl 10/531, the left central dorsal plate 1 of the pectoral fin; LDM Pl 10/532, processus brachialis of the fragmentary anterior ventral lateral plate. From the Kalnamuiža locality on the Amula River, Kurzeme, western Latvia: LDM G 67-1, the left anterior ventral lateral plate

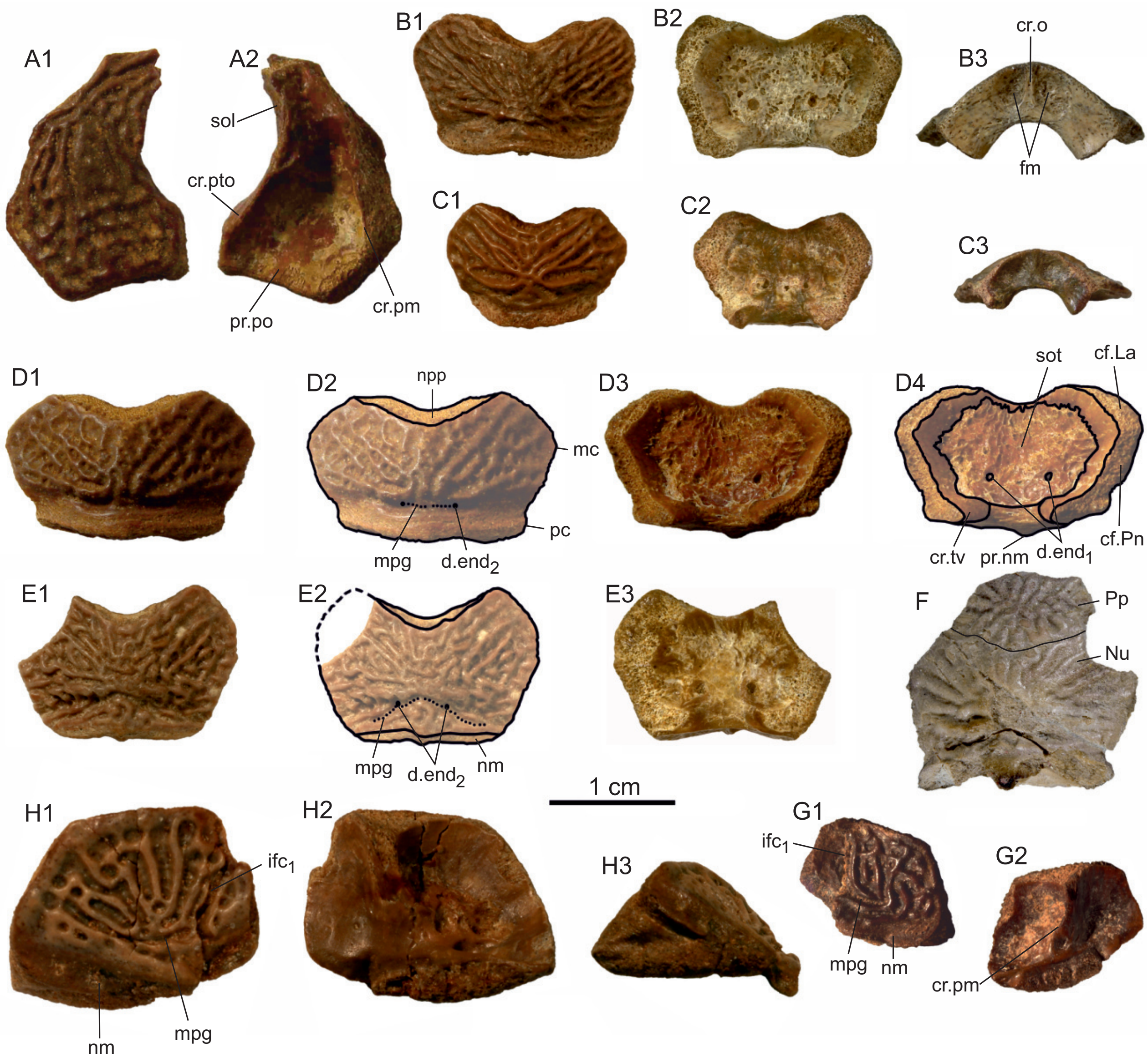

Fig. 3. *Walterilepis speciosa* (Gross) skeletal elements of the head armour. **A**, LDM Pl 10/526, partial left lateral plate in dorsal (A1) and visceral (A2) view; **B**, LDM Pl 10/518, nuchal plate in dorsal (B1), visceral (B2) and posterior (B3) view; **C**, LDM Pl 10/520, nuchal plate in dorsal (C1), visceral (C2) and posterior (C3) view; **D**, LDM Pl 10/523, nuchal plate in dorsal (D1) and visceral (D3) view, as well as labelled drawings in dorsal (D2) and visceral (D4) view; **E**, LDM Pl 10/521, nuchal plate in dorsal (E1) and visceral (E3) view, as well as labelled drawing in dorsal (E2) view; **F**, holotype MB f 136, articulated nuchal and postpineal plates in dorsal view; **G**, LDM Pl 10/525, left paranuchal plate in dorsal (G1) and visceral (G2) view; **H**, LDM Pl 10/524, right paranuchal plate in dorsal (H1), visceral (H2) and posterior (H3) view. A–E, G, H, from the Gurova Ravine; F, from the type locality on the Daugava River close to Bramberģe. Abbreviations: cf.La, area overlapping lateral plate; cf.Pn, area overlapping paranuchal plate; cr.o, median occipital crest; cr.pm, paramarginal crest of head shield; cr.pto, postorbital crest of head shield; cr.tv, transverse nuchal crest; d.end$_1$, ventral foramina of endolymphatic ducts on head shield; d.end$_2$, dorsal foramina of endolymphatic ducts on head shield; fm, insertion fossa on head shield for levator muscles; ifc$_1$, principal section of infraorbital sensory line on head shield; mc, lateral corner of Nu plate; mpg, middle pit-line groove; nm, smooth obtected nuchal area of head shield; npp, postpineal notch in nuchal plate; Nu, nuchal plate; pc, posterolateral corner of Nu plate; Pp, postpineal plate; pr.nm, nuchal process of head shield; pr.po, anterolateral angle of otico-occipital depression of head shield; sol, suborbital lamina of head shield; sot, supraoptic thickening.

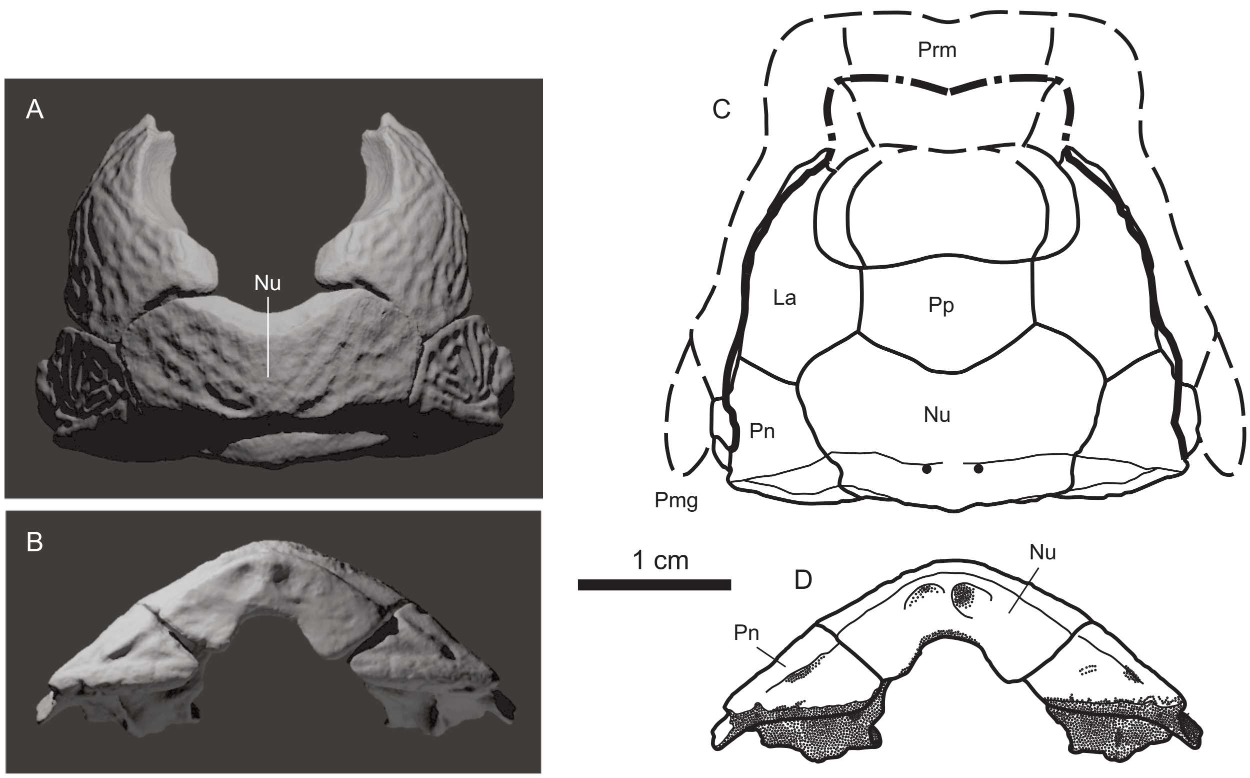

Fig. 4. A, **B**, model of the partial head shield of *Walterilepis speciosa* (Gross) based on the photogrammetric models of the left La plate LDM Pl 10/526 and its mirror image as the right La plate, the Nu plate LDM Pl 10/523, the right Pn plate LDM Pl 10/524 and its mirror image as the left Pn plate. All specimens from the Gurova Ravine. **C**, **D**, tentative reconstruction of the head shield of *Walterilepis speciosa* (Gross) based on the model and the holotype MB f 136, in dorsal (C) and posterior (D) view. Abbreviations: La, lateral plate; Nu, nuchal plate; Pmg, postmarginal plate; Pn, paranuchal plate; Pp, postpineal plate; Prm, premedian plate.

(holotype of *Asterolepis*? *amulensis*). From the Langsēde locality on the Imula River, Kurzeme, western Latvia: LDM G 99/50, a right anterior ventral lateral plate; LDM G 99/51, a posterior median dorsal plate; NRM-PZ P4586, a partial anterior median dorsal plate.

Type locality. Outcrop at the left bank of the Daugava River near Bramberģe, Daugmale Parish, central Latvia. Note that the level of the Daugava River has risen due to the construction of the dam of the Riga hydroelectric station, thus the main part of the type locality nowadays is below the water level.

Emended diagnosis. A small pterichthyodid with a dorsal length of head and trunk-shields reaching at least 60 mm. The Nu plate is quite strongly vaulted, with breadth/length index of 1.42–1.70. The endolymphatic ducts open not far from each other. The posterior margin of the Nu plate bears a pointed posterior projection. The pits for insertion of the head muscles are well pronounced on the high posterior wall of the Nu plate. The triangular incision for the postpineal is not deep. The anterior margin of the Pp plate is narrower than the posterior margin. The posterior wall of the Pn plate is very high. A high trunk-shield has strongly arched dorsal wall and flat ventral wall. The AMD plate with a high dorsal crest caudally from the tergal angle. PMD plate high and short, and conical in shape, with the dorsal crest in the anterior third of the plate. Lateral lamina of the AVL plate is highest at the anterodorsal corner; it is higher than the ventral lamina is wide; lateral lamina about 1.6–1.8 times as long as high, with a short posterodorsal contact face for the MxL plate. The angle between the ventral and lateral laminae reaches 90°–100°. The foramen axillare is very small, smaller than 1 mm, oval; it opens dorsally on the visceral surface of the AVL plate. The plates of the head shield and dorsal trunk armour are ornamented with smooth, radially arranged tubercles; the AVL plate is weakly ornamented with very low and smooth radiating ridges.

Description

Head

Walterilepis was a small pterichthyodid. The available material indicates a similar maximum size to *Gerdalepis*

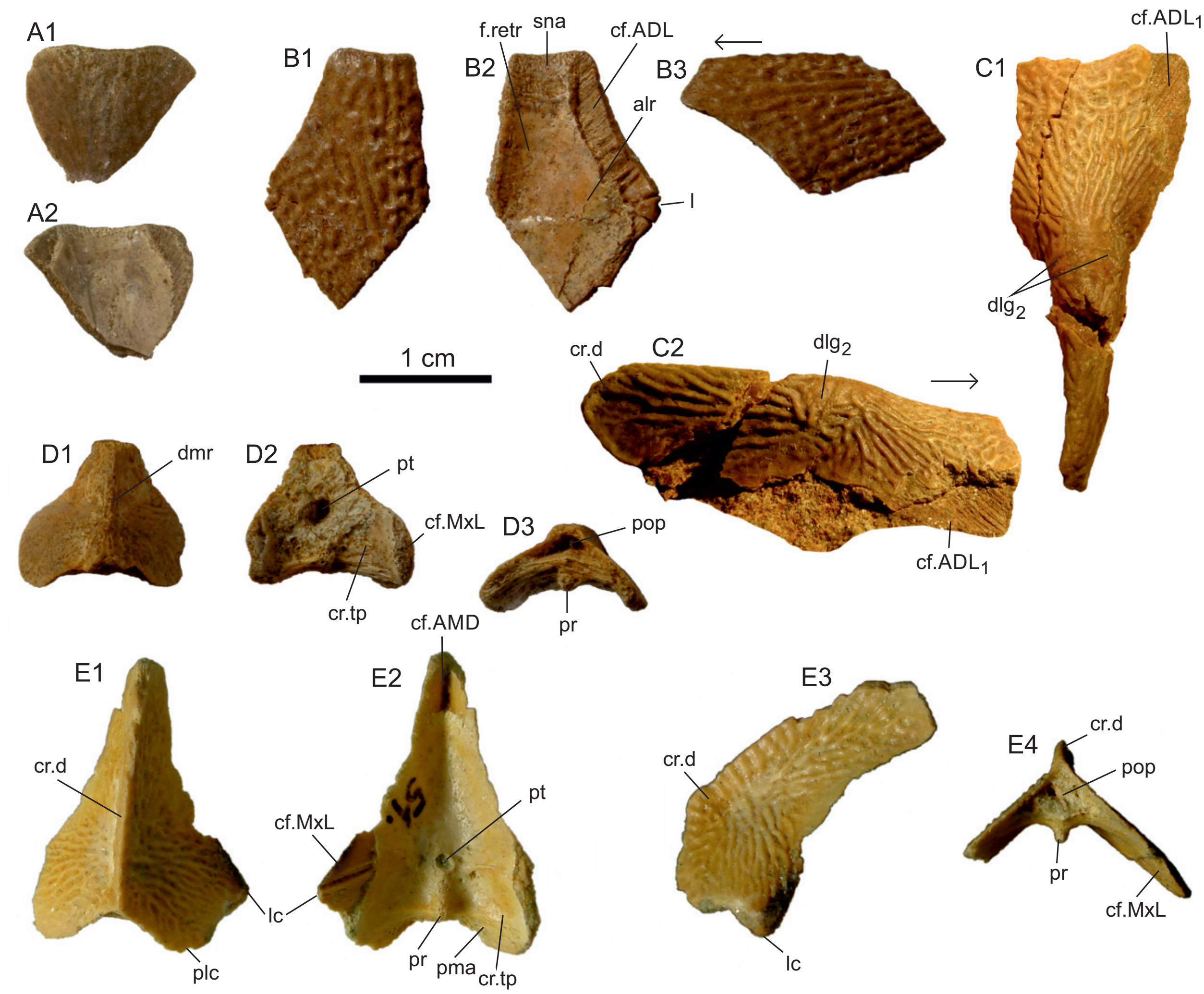

Fig. 5. *Walterilepis speciosa* (Gross) skeletal elements of the dorsal part of the trunk armour: **A**–**C**, partial AMD plates: A, LDM Pl 10/527, in dorsal (A1) and visceral (A2) view; B, LDM Pl 10/533, in dorsal (B1), visceral (B2) and left lateral (B3) view; C, NRM-PZ P4586, in dorsal (C1) and right lateral (C2) view; **D**, **E**, partial PMD plates: D, LDM Pl 10/528, in dorsal (D1), visceral (D2) and posterior (D3) view; E, LDM G 99/51, in dorsal (E1), visceral (E2), right lateral (E3) and posterior (E4) view. A, B, D, from the Gurova Ravine; C, E, from the Langsēde locality at the Imula River. Abbreviations: alr, anterolateral ridge on AMD; cf.ADL, area overlapping ADL; cf.ADL$_1$, imprint of area overlapping ADL; cf.AMD, area overlapping AMD; cf.MxL, area overlapping MxL; cr.d, dorsal median crest of trunk shield; cr.tp, internal posterior transversal crest; dlg$_2$, posterior oblique dorsal sensory line groove; dmr, dorsal median ridge of trunk shield; f.retr, levator fossa of AMD; l, lateral corner of AMD; lc, lateral corner of PMD; plc, posterior lateral corner of PMD; pma, posterior marginal area of PMD; pop, posterior pit of PMD; pr, posterior ventral process of PMD; pt, posterior ventral pit of dorsal wall of trunk shield; sna, supranuchal area. Arrows point anteriorly.

rhenana, *Pterichthyodes milleri* or *Sherbonaspis andreannae* (Gross 1941; Hemmings 1978; Panteleyev 1993). *Byssacanthus dilatatus*, *Stegolepis jugata*, *Gerdalepis dohmi* and *Sherbonaspis hillsi* were somewhat larger species (Karatajūtė-Talimaa 1960; Denison 1978; Young & Gorter 1981). Of the dermal bones of the head shield only the postpineal, nuchal, paranuchal and partial lateral plates are known (Fig. 3).

The tentative 3D reconstruction of the head produced using Blender 2.74 (Fig. 4) suggests that the head shield was rather vaulted, relatively long and narrow; most probably it was longer than broad. The orbital fenestra of the model is relatively large and broad; the anterior portion of the head shield is about half as long as the posterior portion.

Postpineal plate (Pp). The only known Pp plate (MB f 136) is wider than long with a B/L index of 1.78 (Fig. 3F). The lateral margin contacting with the La plate is long, thus the plate is relatively more elongated than the Pp plate in

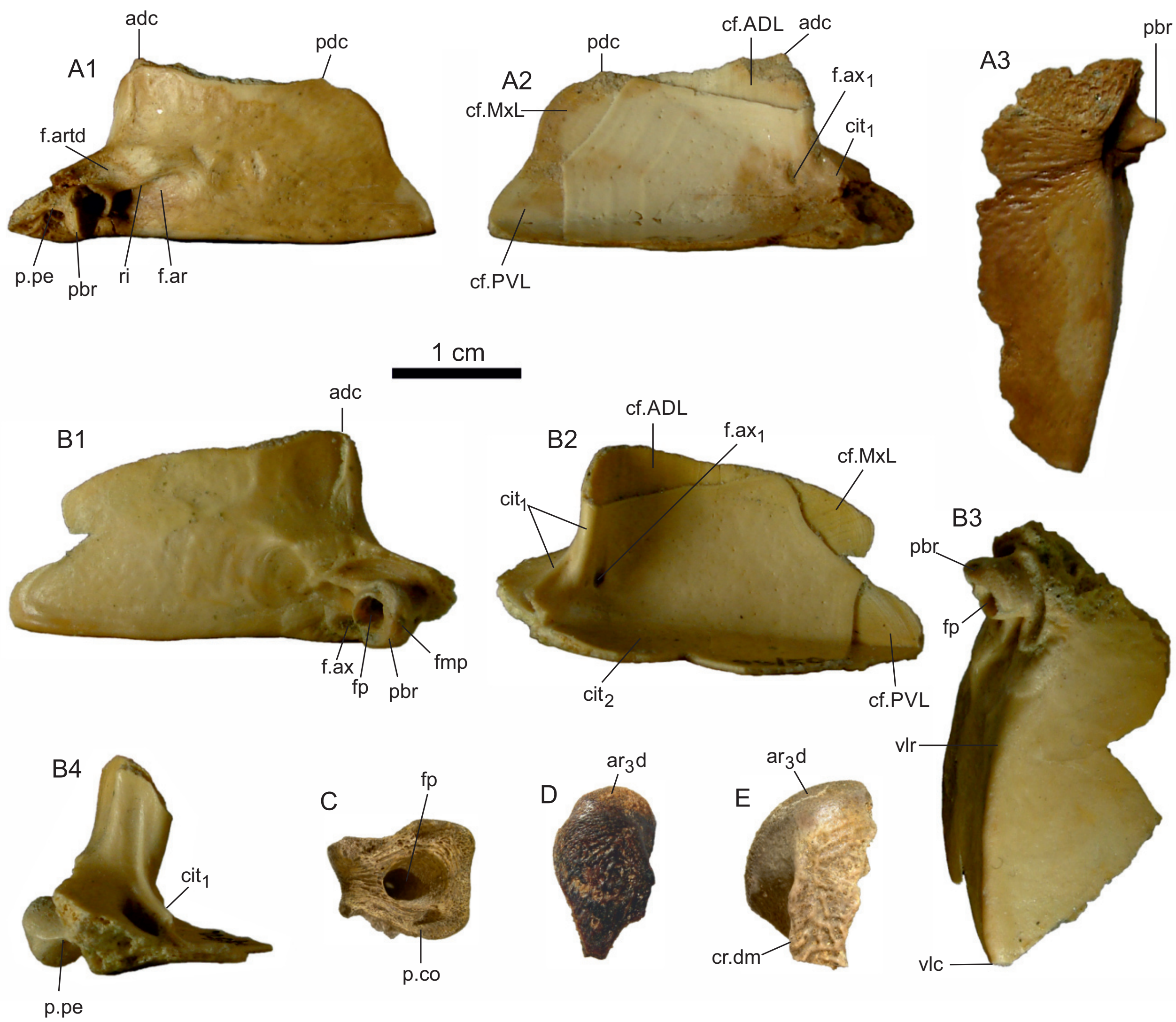

Fig. 6. *Walterilepis speciosa* (Gross) skeletal elements of the ventral part of the trunk armour (**A**–**C**) and pectoral appendage (**D**, **E**): A, left AVL LDM G 67/1, in lateral (A1), visceral (A2) and ventral (A3) view; B, right AVL LDM G 99/50, in lateral (B1), visceral (B2), ventral (B3) and anterior (B4) view; C, partial processus brachialis of the AVL LDM Pl 10/532 in posterior view; D, LDM Pl 10/531, left central dorsal plate 1 in dorsal view; E, LDM Pl 10/530, partial right central dorsal plate 1 in dorsal view. A, B, from the Langsēde locality at the Imula River; C–E, from the Gurova Ravine. Abbreviations: adc, anterodorsal corner of AVL plate; ar_3d, external articular area of Cd_1; cf.ADL, area overlapping ADL; cf.MxL, area overlapping MxL; cf.PVL, area overlapping PVL; cit_1, postbranchial crest (anterior division of crista transversalis interna anterior); cit_2, posterior division of crista transversalis interna anterior; cr.dm, dorsomesial crest of pectoral fin; f.ar, articular facet; f.artd, dorsal part of pectoral articular fossa; f.ax, axillary foramen; f.ax_1, opening of axillary foramen on visceral surface; fmp, protractor area of brachial process; fp, funnel pit; p.co, pars condyloidea; pdc, posterodorsal corner of AVL plate; p.pe, pars pedalis of brachial process; pbr, processus brachialis; ri, ridge on AVL plate; vlc, ventrolateral corner; vlr, ventrolateral ridge.

Byssacanthus, *Pterichthyodes* and *Stegolepis* (Karatajūtė-Talimaa 1960; Malinovskaya 1973; Hemmings 1978). The anterior margin is slightly convex, and it is shorter than the maximum width of the plate along the posterior lateral corners. Hence the anterior lateral margins are oblique, forming an acute angle with the right and left portions of the posterior margin. The anterior margin shorter than the maximum breadth of the plate occurs also in the Pp plate of *Pterichthyodes* (Hemmings 1978, text-fig. 1B, C); however, its lateral margin is always very short and never forms an acute angle with the posterior margin. The posterior margin in *Walterilepis* forms a shallow V-shape, strongly differing in shape from all other pterichthyodids. Smooth rounded ridges radiate from the centre of the plate.

Nuchal plate (Nu). The nuchal plate (Fig. 3B–F) is morphologically variable but usually its shape resembles that of the Nu plate in some species of *Asterolepis* (Karatajūtė-Talimaa 1963; Lyarskaya 1981) and *Sherbonaspis* (Young & Gorter 1981). The Nu plate is well preserved in LDM Pl 10/518 and 10/523 (Fig. 3B, D). The plate is rather strongly vaulted; it is short and wide with a B/L index of 1.42–1.70 (1.54 on an average of six measured specimens) at the lateral corners (1.63 in the holotype). It is proportionately shorter and broader than in *Gerdalepis*, *Stegolepis jugata* and *Sherbonaspis* (Gross 1941; Malinovskaya 1973; Young & Gorter 1981; Panteleyev 1993), but similar to that of *Byssacanthus* (Karatajūtė-Talimaa 1960) and relatively longer and narrower than that in *Pterichthyodes* (Hemmings 1978). The lateral corners are situated anteriorly from the middle of the length of the lateral edges so that the anterior division of the lateral margin is 1.4–2.3 times shorter than the posterior lateral division. This feature is similar to *Sherbonaspis hillsi* (Young & Gorter 1981). The occipital (posterior) margin usually is slightly concave or almost straight (holotype). It is slightly longer than the anterior margin and 1.28–1.41 times shorter than the maximum breadth through the lateral corners. A relatively short, smooth obtected nuchal area continues along this margin. The bone has a small sharp posterior middle projection. The rounded triangular notch for the Pp plate is shallow, not reaching posteriorly the line crossing the lateral corners of the Nu plate. The external openings of the endolymphatic ducts ($d.end_2$) are very small, sometimes not well seen (e.g. in LDM Pl 10/523, Fig. 3D), and relatively closely spaced (about 3.5–5.6 mm apart). Gross (1933a) noted the absence of sensory line canal grooves in the holotype, where neither the middle pit-line groove nor the V-shaped central sensory line canal is visible (Fig. 3F). This can partly be explained by the poor preservation of the holotype, because the middle pit-line groove (mpg) is well discernible in the newly collected material. Usually it is represented by short branches between the endolymphatic duct openings, however, in LDM Pl 10/521 it continues also laterally from the openings (Fig. 3E) but not reaching the posterolateral margin. On the posterior wall of the plate, the paired parasagittal fossae lateral to the median occipital crista (moc) are relatively large and deep (Fig. 3B3, C3). These were interpreted by Stensiö (1931) to be attachment areas for the cranial levator muscles. The internal surface of the plate exhibits a rough large supraotic thickening (sot). The internal foramina of the endolymphatic ducts ($d.end_1$) are large (Fig. 3D3, D4) and between 2.9 and 5.0 mm apart. Sometimes the distance is slightly shorter than between the external foramina. The tubercles on the outer surface form ridges in rows radiating from the centre point of the plate.

Paranuchal plate (Pn). The Pn plate (Fig. 3G, H) is subsquare in shape, with the maximum width in its posterior part slightly exceeding the length. The B/L index is 1.12–1.34 (measured in two specimens). The posterior margin of the bone is slightly convex, with a wide and well-developed smooth obtected nuchal area. The middle pit-line groove (mpg) is short and weakly seen. The lateral segment of the bone is 0.35–0.49 times as wide as the medial segment. The posterior wall is very high, much higher than in *Asterolepis*. The internal surface shows a very high paramarginal crest (cr.pm) dividing the surface into two regions approximately equal in width. The posterolateral corner of the otico-occipital depression is rounded. The external ornamentation consists of vermiculating ridges and pits.

Lateral plate (La). The single lateral plate (LDM Pl 10/526) is incomplete, missing the anterior part, but the orbital, lateral, posterolateral and posteromesial margins are well preserved. As reconstructed (Fig. 4) the plate is about twice as long as broad. The preserved length is 21.2 mm. The plate is thickest (6.0 mm) at the middle of the orbital margin. The preserved part of the paramarginal crest (cr.pm) is so situated as to suggest a quite lateral position for the infraorbital sensory canal, with a correspondingly narrow lateral division of the bone, as in all asterolepidoids (Stensiö 1938, p. 82). In its elongate shape the specimen resembles the La plate of *Asterolepis* or *Pterichthyodes* and differs from *Stegolepis jugata* (Malinovskaya 1973, fig. 1, p. 74) with a much broader plate. The prominent postorbital crest (cr.pto) continues beneath the orbital opening as a high suborbital lamina (sol), but there is no indication of a lateral division of the preorbital recess, a characteristic feature of *Bothriolepis* (Stensiö 1948, p. 49). The postorbital crest (cr.pto) is much closer to the orbital margin than in *Sherbonaspis* (Young & Gorter 1981, fig. 13) or *Asterolepis* (Lyarskaya 1981, fig. 71). Judging from the structure of the posteromesial margin, the postorbital crest extended posteriorly onto the Pp and Nu plates along the suture between these plates, and not onto the Nu plate as in bothriolepids and *Pterichthyodes* (see Hemmings 1978, p. 13), nor onto the Pp plate as in *Asterolepis* (Lyarskaya 1981, fig. 68) and presumably *Sherbonaspis* (Young & Gorter 1981). The Pp plate overlaps the La plate along a substantially longer section of its margin than in *Pterichthyodes* (Hemmings 1978, text-figs 1, 2), but in this respect is similar to *Asterolepis* (e.g. Lyarskaya 1981, figs 62, 68). The paramarginal crest is moderately high and lower than the postorbital crest, thus differing from its form in *Asterolepis* (e.g. Lyarskaya 1981, fig. 71). The external ornamentation consists of vermiculating ridges running in rows parallel to the lateral edge in the lateral part of the plate and a fine meshed network of pits in the medial part of the plate.

Trunk shield

Anterior median dorsal plate (AMD). Only three specimens are known: LDM Pl 10/527 (Fig. 5A) from a smaller individual, LDM Pl 10/533 (Fig. 5B) and NRM-PZ P4586 (Fig. 5C) from slightly larger individuals. All are very incomplete, so the proportions of the plate cannot be estimated. However, the plate seems relatively shorter and broader than that of *Pterichthyodes* and *Sherbonaspis* (Hemmings 1978, text-fig. 9; Young & Gorter 1981, fig. 15A). The AMD plate is strongly vaulted, with the dorsal median ridge seen in LDM Pl 10/527 as a slight elevation along the posterior broken margin. There is a high and well-pronounced keel in NRM-PZ P4586 (Fig. 5C). The anterior margin is concave, as is the anterior lateral margin that formed a contact with the ADL plate. The visceral surface of LDM Pl 10/533 (Fig. 5B) shows a distinct supranuchal area (sna), and a very low anterolateral ridge (alr) bordering a long narrow depressed area corresponding to the levator fossa in *Bothriolepis* (f.retr). This is developed similarly to *Sherbonaspis* (Young & Gorter 1981, fig. 15A). The area overlapping the anterior dorsal lateral plate (cf.ADL) is narrow, terminating posteriorly from the lateral corner (l). Smooth rounded ornamental ridges radiate from the ossification centre of the plate on the outer surface. Two short branches of the posterior oblique dorsal sensory line groove are weakly developed in NRM-PZ P4586, as in some species of *Asterolepis* (e.g. *Asterolepis* sp. 1 and *Asterolepis ornata*: Lyarskaya 1981).

Posterior median dorsal plate (PMD). The three known PMD plates (Fig. 5D, E) are rather incomplete, but all are preserved in three dimensions. LDM G 99/51 is the most complete (Fig. 5E), with a B/L index of 0.87. Thus, the plate was high and moderately short, like the PMD plate in *Gerdalepis rhenana* (Gross 1941). The dorsal median ridge is developed as a moderately high crest (cr.d, Fig. 5E3) along the whole length of the plate, and would have been continuous with that on the AMD plate. The posterior margin is concave with no posterior angle, resembling that in *Pterichthyodes* (Hemmings 1978, text-fig. 10). This margin is swollen due to the crest of the dorsal median ridge and shows the posterior pit between the dorsal surface of the plate and the transverse posterior crest on the internal surface (cr.tp). However, the structure of the posterior margin differs from that in *Gerdalepis*, *Grossaspis* and *Lepadolepis* in the absence of regular, prismatic spongiosa (cf. Gross 1965). The dorsal surface shows the network of low anastomosing ridges radiating from the posterior central part of the plate. The visceral surface of LDM G 99/51 (Fig. 5E2) shows the two overlapping areas for the mixilateral plates (cf.MxL) on the lateral edges, but both are broken and incomplete. The contact face overlapping the AMD (cf.AMD) along the anterior edge of the PMD plate is partially preserved only in LDM G 99/51. The transverse posterior internal crest (cr.tp) is low, with a slight anterior curvature reflecting the concave posterior margin of the plate. This crest bears a prominent, sharp conical tubercle (pr) in the middle, and a deep ventral funnel pit (pt) is well developed anteriorly from the crest. The posterior marginal area (pma) is narrow in the middle and expanded at the lateral margins.

Anterior ventral lateral plate (AVL). Two relatively well preserved AVL plates are known from Kurzeme. The left AVL plate LDM G 67/1 was previously described as the holotype of *Asterolepis*? *amulensis* Lyarskaja (Fig. 6A). LDM G 99/50 (Fig. 6B) is a right AVL plate, and one broken processus brachialis of the AVL plate LDM Pl 10/532 comes from the Gurova site (Fig. 6C). Specimen LDM G 67/1 was erroneously mentioned and figured as a right AVL plate by Lyarskaya (1981, p. 137; fig. 104, a mirror image; compare with the photo of this specimen in Lyarskaya's plate XXXVII, fig. 5). The two complete AVL plates are of similar size (length 35.3 mm in LDM G 67/1 and 34.7 mm in LDM G 99/50). The processus brachialis LDM Pl 10/532 is from a much larger individual. All margins of the lateral lamina in the two complete plates are well preserved, except for a slightly damaged posterior edge in LDM G 99/50. In contrast, the margins of the ventral lamina are damaged, particularly in LDM G 67/1, probably because these edges were very thin. The angle between ventral and lateral laminae is 90° in LDM G 99/50 and 100° in LDM G 67/1. The lateral lamina is higher than the ventral lamina is wide, suggesting a rather high and narrow trunk shield in *Walterilepis speciosa*, resembling that of *Byssacanthus* (Karatajūtė-Talimaa 1960), and differing from the proportions in *Asterolepis*, *Stegolepis* and *Sherbonaspis* (e.g. Malinovskaya 1973, p.76; Lyarskaya 1981; Young & Gorter 1981). In the latter forms the ventral lamina is wider than the lateral lamina is high. The ventral lamina of the plate is elongate (B/L index about 0.41 in LDM G 99/50). The ventral lamina is flat, as in *Byssacanthus*, *Stegolepis* and *Sherbonaspis*, and in contrast to *Gerdalepis*. The subcephalic division is relatively short, probably comprising about 22–24% of the length of the ventral lamina, but the anterior margin in LDM G 99/50 is damaged so a precise measurement is impossible. The anterolateral corner of the anterior margin and the notch for the semilunar plate are not well preserved. The left AVL plate probably overlapped the right one. The lateral margin is slightly convex in both specimens. The area overlapping the median ventral plate is missing in both specimens. The area overlapping the posterior ventral lateral plate (cf.PVL) is rather long; the ventrolateral corner (vlc) is sharp and well pronounced. The ventrolateral ridge (vlr) is sharp along the subcephalic division and rounded but well developed along the remaining length of the plate (damaged in the anterior part of LDM G 99/50). The ventral division of the crista transversalis interna anterior is very high laterally and immediately decreases in height mesially. As in *Asterolepis* and *Pterichthyodes* (Hemmings 1978, p. 23), but in contrast to *Sherbonaspis* (Young & Gorter 1981, fig. 18), it is divided into anterior and posterior branches. The anterior branch (cit_1) is sharp-edged and high laterally but decreases in height anteromesially. The posterior branch (cit_2) forms a very low rounded ridge mesially.

The lateral lamina of the AVL plate is about 1.6–1.8 times as long as high, thus being proportionately higher even than in *Byssacanthus* (Karatajūtė-Talimaa 1960, pl. 3, fig. 2). It is highest at the anterodorsal corner (adc), in contrast to *Pterichthyodes* (Hemmings 1978, figs. 13, 14), *Stegolepis* (Malinovskaya 1973, p. 77) and *Sherbonaspis* (Young & Gorter 1981, fig. 18, p. 106) where it is highest at the posterodorsal corner. The dorsal margin is slightly concave. The area overlapping the anterior dorsal lateral plate (cf.ADL) is wide anteriorly and tapers posteriorly, passing into the posterodorsal area overlapping the mixilateral plate (cf.MxL). This continues ventrally into the posterior area overlapping the posterior ventral lateral plate (cf.PVL).

The foramen axillare (f.ax) is very small, only 0.7 mm × 0.5 mm in LDM G 67/1. It is oval as in *Pterichthyodes* (Hemmings 1978, p. 31) rather than subcircular as in *Sherbonaspis* (cf. Young & Gorter 1981, p. 106). The axillary foramen on the visceral surface ($f.ax_1$) opens dorsally, rather than mesially as in *Asterolepis ornata* Eichwald (pers. observation). The brachial process (pbr) in the three preserved examples shows the articular facet (f.ar) which is rather small and weakly defined caudally from the processus brachialis. It is more clearly delimited dorsally by a low crest, which separates the articular facet from the dorsal part of the pectoral articular fossa (f.artd). This crest is better preserved in LDM G 99/50. The prepectoral corner is damaged in all specimens. The pars condyloidea (p.co) of the brachial process is of rounded triangular shape, as is typical in asterolepidoids (cf. Lyarskaya 1981, fig. 86). The wide and flat triangular protractor area (fmp) is oriented anteriorly; the pars pedalis (p.pe) in front of this area is very narrow.

The AVL plates are weakly ornamented, with very low and smooth ridges radiating mesially and caudally from the articular pectoral fossa on the ventral lamina, and a fine-meshed network in the anterior part of the lamina. The lateral lamina is almost smooth, with faint ridges seen only in the very oblique light. The ornamentation of the AVL plate in *Walterilepis* resembles that of the PVL plate and other skeletal elements in *Asterolepis syasiensis* (Lyarskaya 1981, pp. 133–136).

Pectoral appendages. Only two disarticulated dorsal central plates 1 (Cd_1) are known from the pectoral appendage. The Cd_1 is about 1.8 times as long as broad at the broadest point in LDM Pl 10/531 (Fig. 6D) and is therefore slightly longer and narrower than in *Sherbonaspis* (Young & Gorter 1981, p. 107). This is within the interval of variability for *Pterichthyodes* (Hemmings 1978). The dorsal lamina is widest in the proximal part, as in *Sherbonaspis* (Young & Gorter 1981, fig. 18D, E), and contrary to *Pterichthyodes* (Hemmings 1978, text-fig. 20). It sutures with the lateral marginal plate 2 (Ml_2), mesial marginal plate 1 (Mm_1), mesial marginal plate 2 (Mm_2) and dorsal central plate 2 (Cd_2). The dorsomesial crista (cr.dm) is quite distinct but is smooth without any spines along the edge (Fig. 6E). The mesial lamina lacks ornament, as in *Asterolepis* and *Sherbonaspis*, but on the dorsal lamina it consists of rows of elongated tubercles and low ridges radiating from the most proximal mesial point.

DISCUSSION

Morphology and systematics

The basis on which *Walterilepis speciosa* is referred here to the Pterichthyodidae requires some comment. Gross, with only the Nu and Pp plates available for the study, initially placed '*Taeniolepis*' (now *Walterilepis*) among the Antiarchi incertae sedis (Gross 1933a). Gross (1965) revised this opinion and referred '*Taeniolepis*' to the Asterolepiformes incertae familiae. The suborder Asterolepidoidei (family Asterolepidae of Denison 1978) is one of three widely accepted higher taxa within the order Antiarcha. Denison (1978) did not recognize a pterichthyodid grouping and listed six genera in his 'family Asterolepidae' (*Asterolepis*, *Byssacanthus*, *Gerdalepis*, *Pterichthyodes*, *Remigolepis* and *Stegolepis*). Denison (1978) listed other forms as Antiarchi incertae sedis (e.g. *Lepadolepis* and *Taeniolepis*). New genera described since then include *Sherbonaspis* Young & Gorter (1981), *Pambulaspis* Young (1983) and *Wurungulepis* Young (1990). A broad and long trunk shield distinguishes the genera *Asterolepis* and *Remigolepis* from other asterolepidoids that have a high and short trunk shield composed of proportionally broader plates (exemplified by *Pterichthyodes*, *Byssacanthus* or *Gerdalepis*). On this basis two families can be distinguished, namely the Asterolepididae and Pterichthyodidae, the latter previously proposed by Stensiö (1948) and later accepted by various authors (Karatajūtė-Talimaa 1960; Hemmings 1978; Young & Gorter 1981; Young 1990; Moloshnikov 2008). However, the detailed character analysis based on a comprehensive character matrix of antiarchs (Zhu 1996) supported the opinion that Pterichthyodidae is a paraphyletic (Janvier & Pan 1982) or even polyphyletic grouping (Zhu 1996). The presence of an apical chamber, a single semilunar plate and the characteristic shape of the armour of *Gerdalepis* were used to classify this genus in a separate subfamily by Stensiö (1948). This classification was accepted by Gross (1965), Miles (1968) and Hemmings (1978). Friman (1982) recognized two pterichthyodid subfamilies (of three asterolepid subfamilies in Miles 1968): Pterichthyodinae containing *Pterichthyodes* and *Byssacanthus* and Gerdalepidinae containing *Gerdalepis*, *Grossaspis* and *Lepadolepis*. Zhu (1996) united the three latter genera into the family Gerdalepididae. This family is characterized by the similar dorsal spongy layer in the dermal bone of the trunk shield. However, this subdivision is not well supported as the taxa are rather poorly known. Besides, *Walterilepis* shows no spongy layer in the PMD and AVL plates, and the presence of this feature in the AMD plate is unknown. Long's (1983) antiarchs classification lists the following genera belonging to the family Pterichthyodidae: *Pterichthyodes*, *Sherbonaspis*, *Stegolepis*, *Gerdalepis*, *Lepadolepis*, *Grossaspis* and *Byssacanthus*. Later *Wurungulepis* was also demonstrated to belong to the Pterichthyodidae (Young 1990).

Walterilepis speciosa is not readily compared with other genera within the Asterolepidoidea because of the limited available material. However, the broad AMD and PMD plates with a distinct dorsal crest, a strongly vaulted Nu plate, a very high posterior wall of the Pn plate and a relatively high AVL plate suggest a high and short trunk shield with a well-developed dorsal median crest. Thus, *Walterilepis* clearly differs from the Asterolepididae characterized by a low and long trunk shield. All the above-mentioned features clearly indicate that *Walterilepis* should be assigned to the Pterichthyodidae. A high and short trunk shield could be the synapomorphy uniting *Walterilepis* with the other Pterichthyodidae.

Pterichthyodes, *Byssacanthus*, *Sherbonaspis* and *Stegolepis* are the best described genera within the Pterichthyodidae (Karatajūtė-Talimaa 1960; Malinovskaya 1973; Hemmings 1978; Young & Gorter 1981; Panteleyev 1993). Detailed comparison with *Walterilepis* shows a small number of resemblances to *Pterichthyodes*: the similar small maximum size of the armour, the shape of the La plate, the shape of the posterior margin of the PMD plate and the oval shape of the axillary foramen. *Walterilepis* differs readily from *Pterichthyodes* and *Byssacanthus* in the presence of a high and well-pronounced keel on the AMD plate; it differs also from *Pterichthyodes* in the following: the more elongated Pp plate with a very long lateral margin of the plate, the longer and narrower Nu plate, the position of the postorbital crest on the posterior part of the La plate, the relatively shorter and broader AMD plate, the shape and proportions of the lateral lamina of the AVL plate and the proportion of the dorsal lamina of the dorsal central plate 1. *Byssacanthus* differs from *Walterilepis* in having a dorsal median spine instead of a dorsal median keel; it differs also in a much larger size, in the relatively shorter Pp plate and many other features concerning the shape and proportions of the trunk shield plates.

Walterilepis resembles *Sherbonaspis* in the presence of a dorsal median crest on the AMD and PMD plates and the shape of the Nu plate. *Walterilepis* differs clearly from *Sherbonaspis* in the following: its relatively shorter and broader AMD plate, the proportions of a more elongated ventral wall of the trunk shield, the much shorter branches of the middle pit-line groove of the Nu plate, the shape and proportions of the lateral lamina of the AVL plate and the division of the internal transverse crest into two branches. Besides, *Sherbonaspis hillsi* is a much larger species than *Walterilepis speciosa*. However, *Sherbonaspis andreannae* is of a similar maximum size as *Walterilepis* (Panteleyev 1993). *Walterilepis* differs from *Stegolepis* in almost all aspects of its morphology except the radially arranged ornamentation. However, in *Stegolepis* it consists of ridges, whereas in *Walterilepis* it is composed of the radially arranged tubercles, rather smooth on the lateral wall of the trunk shield. Relevant here is the suggestion by Janvier & Pan (1982) that the genera *Stegolepis* and closely similar and related *Hunanolepis* from China (Wang 1991; Young 1993) may be more primitive than other known pterichthyodids, including *Pterichthyodes* and *Sherbonaspis*, even though these have been found from younger strata (Givetian/Frasnian).

Walterilepis shows many similarities with *Gerdalepis rhenana*, including a similar maximum size (*G. dohmi* (Gross, 1933) is a much larger species; *G. jesseni* Friman, 1982 is of a similar size as *G. rhenana*), the presence of the median dorsal crest forming a keel on the AMD and PMD plates, the shape and proportions of the PMD plate, the proportions of the lateral lamina of the AVL plate and the tuberculated ornamentation. *Walterilepis* differs from *Gerdalepis* in the absence of regular, prismatic spongiosa along the posterior margin of the PMD plate, in the flat ventral lamina of the AVL plate (convex in *Gerdalepis*) and in the shorter and broader Nu plate. Evidence on the cross-section shape of the trunk shield in *Walterilepis* is limited; it is triangular in *Gerdalepis*, with an acute dorsal median crest, but this is not the case in *Walterilepis*. Despite the limited material for the comparison, *Walterilepis* demonstrates strong similarity with *Lepadolepis* from Germany (Gross 1933b) in the trunk shield morphology although the trunk shield is slightly larger in *Lepadolepis*. Due to the limited material of *Lepadolepis*, it is difficult to make more detailed comparisons. The head shield of *Lepadolepis* is unknown, so on available evidence no conclusion can be drawn as to whether these two genera are synonymous or only closely related.

Biostratigraphy, biogeography and palaeoecology

As noted above, at least six taxa of antiarch placoderms have been previously listed from the Ogre Formation, namely *Bothriolepis maxima*, *B. evaldi*, *Asterolepis*? *amulensis* (referred here to *Walterilepis*), *Grossilepis spinosa*, *Walterilepis speciosa* and Antiarchi gen. et sp. indet. (Gross 1942). Such a total number of antiarch taxa is unusually high for a relatively thin lithostratigraphic unit which formed within a rather short time span most probably corresponding to about one third of the *rhenana* conodont Zone (Lukševičs 2001). The above revision of asterolepidoid material from the Ogre Formation places it all in one species *Walterilepis speciosa*, representing the youngest record to date of asterolepidoids in the Baltic Devonian Basin. Thus, four antiarch species from this formation are comparable to other formations in the Baltic Devonian Basin, e.g., three from the Amata Formation (*Asterolepis radiata*, *Bothriolepis prima* and *B. obrutschewi*) and the Pļaviņas Formation (*Asterolepis radiata*, *Bothriolepis cellulosa* [or vicariant species *B. traudscholdi* in NW Russia] and *Grossilepis tuberculata*; Lukševičs 2001).

Many forms of the Pterichthyodidae are known from Eifelian and Givetian strata, including *Byssacanthus* in the Baltic States and NW Russia, *Pterichthyodes* in Scotland, *Gerdalepis* and *Grossaspis* in Germany and Belgium, *Wurungulepis* and *Sherbonaspis hillsi* in Australia, *Stegolepis* and *Sherbonaspis andreannae* in Kazakhstan, *Hunanolepis* in China (for ages see Gross 1965; Malinovskaya 1973; Hemmings 1978; Lyarskaya 1978; Young & Gorter 1981; Wang 1991; Panteleyev 1993). The diversity of younger pterichthyodid antiarchs is much more restricted and yields *Lepadolepis* from the Upper Frasnian Kellwasserkalk of the Manticoceras Beds, Bad Wildungen, Germany (Gross 1933b). The occurrence of *Lepadolepis* most probably coincides with the Upper Kellwasser Horizon and hence the *linguiformis* conodont Zone (e.g. Feist & Schindler 1994). Thus *Lepadolepis* is only slightly younger than *Walterilepis*, which is consistent with the suggestion that these genera are closely related. The distribution of *Walterilepis*, *Gerdalepis* and *Lepadolepis* suggests also a closer palaeogeographical connection between the Baltic Devonian Basin and Rheinisches Schiefergebirge during the early Late Devonian.

As noted above, *Walterilepis* comes from siliciclastic deposits of unknown facies close to Bramberģe in central Latvia and from tidally influenced sandstone in western (Langsēde locality) and eastern Latvia (Gurova Ravine). The pterichthyodids *Gerdalepis*, *Lepadolepis* and *Grossaspis* come from typical marine facies (Denison 1978), and the occurrence of the above-mentioned antiarchs in marine and deltaic or estuarine facies may indicate that the youngest pterichthyodid representatives of the Asterolepidoidei inhabited the shallow marine rather than the freshwater environment.

CONCLUSIONS

New data on *Walterilepis speciosa* indicate its assignment to the family Pterychthyoididae and probably a close relationship to *Lepadolepis* from the Frasnian of Germany. *Walterilepis speciosa* is so far endemic to the Baltic Devonian Basin, but the distribution of the latest representatives of pterichthyodids suggests closer palaeogeographical connections between the Baltic Devonian Basin and Rheinisches Schiefergebirge during the Frasnian than realized previously.

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Läti Ogre kihistu (Ülem-Devon) antiarhi fossiilide revisjon

Ervīns Lukševičs

Frasnesi lademe (Ülem-Devon) rüükalade hulka kuuluvat antiarhi *Walterilepis speciosa* kirjeldati esmakordselt ühe eksemplari alusel, paigutades ta perekonda *Taeniolepis*. Hiljuti kogutud uus materjal võimaldab selle liigi pead senisest täpsemini kirjeldada. Uus materjal sisaldab ka pektoraaljätkete luid ja kõhurüüd, mis on lühike ning kõrge. Nii pea kui ka kõhurüü kinnitavad, et *Walterilepis* kuulub sugukonda Pterichthyodidae ja on arvatavasti lähisugulane Saksamaa Frasnesi lademes esineva perekonnaga *Lepadolepis*. Kuigi *W. speciosa* on endeemne Balti Devoni settebasseini Läti piirkonnale, viitab ta seniarvatust tihedamatele seostele Reini kildamägede regiooniga. Biostratigraafilisel skaalal asub *Walterilepis* samal tasemel kui *Bothriolepis maxima* ja *B. evaldi*, näidates antiarhide suurt mitmekesisust Pamūšise eal.