Crested antiarch *Bothriolepis zadonica* H.D. Obrucheva from the Lower Famennian of Central European Russia

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New materials on the bothriolepidid *Bothriolepis zadonica* H.D. Obrucheva, 1983 from the Zadonskian Regional Stage (Upper Devonian, Lower Famennian) of Central Devonian Field (Central European Russia) are described and illustrated. These materials came from nine localities in the Orel and Tver Regions of Russia. This species is characterised by the presence of a well developed median dorsal crest in the trunk armour and unusual type of the preorbital recess of the head shield; this recess is designated herein "trapezoid". The ontogenetic and individual variations of *B. zadonica* are studied. The crested bothriolepidids are known only from Euramerica and East Gondwana. The possible relationships between crested bothriolepidids in these provinces are discussed.

Key words: Placodermi, Bothriolepidoidei, *Bothriolepis*, Devonian, Famennian, Russia.

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Introduction

Antiarchs from the Zadonskian Regional Stage of the Central European Russia (Central Devonian Field) are poorly known. The Zadonskian antiarchs were first studied by O.P. Obrucheva and H.D. Obrucheva (1977), who noted the presence of the antiarch *Bothriolepis* sp. nov. Later, H.D. Obrucheva (1980a) suggested that two antiarch species occurred in the two Zadonskian vertebrate localities—quarry of the Lime Factory near the town Livny and site at Rovnechik Creek by village Shilovo: *Bothriolepis* sp. 1 and *Bothriolepis* sp. 2. According to her brief description, *Bothriolepis* sp. 1 was a large bothriolepidid, which has a deep dorsal crest in the trunk armour. The plates of this bothriolepidid are ornamented with large tubercles. *Bothriolepis* sp. 2 was a small bothriolepidid (total length about 20 cm). These are all informations about Zadonskian bothriolepidids in the paper by H.D. Obrucheva. Subsequently, this two antiarch species were named *Bothriolepis* sp. nov. by H.D. Obrucheva (1980b); she suggested that the early definitions of the Zadonskian antiarchs (*B*. sp. 1 and *B*. sp. 2) are incorrect (H.D. Obrucheva 1980b: 95). The author gave a very brief description of *Bothriolepis* sp. nov., but did not formally erect a new species, which was finally named *Bothriolepis zadonica* by H.D. Obrucheva (1983). She described only six plates of this species: nuchal, paranuchal, postpineal, anterior median dorsal, anterior dorso-lateral and mixilateral (about 22 specimens of the head and trunk shields). Moloshnikov (2001a) provided a tentative reconstruction of the head shield and a possible reconstruction of the endocranium.

The main goal of present study is a detailed description of the exoskeleton of *Bothriolepis zadonica* based on the new material.

Material and methods

During 1966, 1976, 1977, 1980, and 1997–2001 the remains of the Zadonskian antiarchs of Central Devonian Field were collected by G. Astrova, I. Chudinova, V. Dobrohotova, N. Krupina, and O. Lebedev. The author of the present paper participated in the field work in 1999 and 2000. The vertebrate remains found in the Zadonskian deposits belong to sarcopterygians, chondrichthyans, acanthodians and placoderms (arthrodires, ptyctodontids, and antiarchs); the antiarch remains prevail among them. This material came from nine localities in the Orel and Tver Regions (Fig. 1): from quarry of the Lime Factory (1) and Kazatskiy (2) quarry near the town Livny, from Livenka River within Livny (3), at Rovnechik Creek by village Shilovo (4), at Lyubovsha River within the town Russkiy Brod (5), Russkiy Brod quarry close to town Russkiy Brod (6), from Tim River in the village Zyabrovo (7), from two boreholes at the village Redkino (8) not far from the city of Tver and at the village Nelidovo (9), Tver Region. Over 400 isolated plates of the head shield, trunk shield and pectoral appendages of the bothriolepidids were collected from these localities.

1) Lime Factory quarry: PrM, 49 specimens; Nu, 48; PNu, 24; PP, 11; L, 33 (complete plates and fragments); PMg, 5; SMg, 1; Ifg, 3 (1 complete plate and 2 fragments); AMD, 10 (complete plates and fragments); PMD, 10 (complete plates and fragments); ADL, 12 (complete plates and fragments); MxL, 6; AVL, 31 (only 1 complete plate); PVL, 1; about 30 fragments of the plates of trunk shield; 62 plates of the armour of pectoral appendages. The antiarch remains are found in the sand and bioaccumulated limestone. The preliminary definition of the accompanying

vertebrates are as follows: *Holoptychius* cf. *nobilissimus* Agassiz, 1839, *Megapomus markovskyi* Vorobyeva, 1977, *Glyptopmus* sp., *Conchodus* sp., *Holodipterus* sp., *Devononchus* sp., ptyctodontids, arthrodires, presumably remigolepids (Moloshnikov 2001b).

2) Kazatskiy quarry: PNu, L and PMg in articulation, 1; AMD, 2; PMD, 1; ADL, 1 fragment; AVL, 2 fragments; PVL, 3 fragments; 4 fragments of the plates of trunk shield and 1 fragment of the plate of pectoral appendage. The antiarch remains are found in the bioaccumulated oolitic limestone.
3) Town Livny, Livenka River: 3 fragments of the plates of trunk shield are found in the limestone.
4) Village Shilovo, Rovnechik Creek: Nu, 6; PNu, 2; AMD, 2; PMD, 1; ADL, 8; MxL, 2; PVL, 1 fragments; 15 fragments of the plates of trunk shield; 1 fragment of the proximal part of the pectoral appendage. These remains were found in the sandy deposits.
5) Town Russkiy Brod, Lyubovsha River: Nu, 2; PMD, 1; 2 fragments of the plates of trunk shield. These plates were found in the sandy and clayey limestone. The antiarchs are found with crossopterygian *Megapomus markovskyi.*
6) Russkiy Brod quarry: AMD and ADL in articulation— 1, which was found in the sandstone.
7) Village Zyabrovo, Tim River: 1 fragment of ADL and 3 fragments of the plates of trunk shield. The vertebrate remains (antiarchs and arthrodires) were found in the oolitic limestone.
8) Borehole at the village Redkino: Nu, 1; 1 fragment of the plate of trunk shield and1 fragment of the plate of pectoral appendage. The plates (of antiarchs and arthrodires) were found in the clay.
9) Borehole at the village Nelidovo: 2 fragments of the plates of trunk shield, which were found in the clay.

The Zadonskian deposits are shallow marine and facially varied in the Central Devonian Field. The Lower Famennian age of these nine vertebrate localities are dated by the invertebrate remains (brachiopods, bivalves, nautiloids, and others), which are present in the limestones and, sometimes, in the sandy deposits, and by conodonts. The detailed evidence of age of these deposits were gave by Rodionova et al. (1995).

The antiarch plates were chemically prepared by dissolving limestone in 10% acetic acid solution and mechanically prepared from sand and sandstone. The head and trunk shields were reconstructed based on the separated plates and the reconstructed head shield is flat.

Measurements of the cranial plates follow the designated points of Stensiö (1948), measurements of the AMD and PMD plates follow Werdelin and Long (1986). All plates names will be abbreviated for convenience (see description and list of abbreviations in Fig. 4), and the words "width", "length" are abbreviated as W and L, respectively; for PrM plate the rostral width is abbreviated as W1, orbital width—W2, and for Nu plate the W1 abbreviates width between posterolateral corners, W2—width between lateral corners, L1—total length of the plate, L2—distance from anterolateral corner to obtected nuchal area; for MxL plate the Wlat—width of the lateral lamina, Wdors—width of the dorsal lamina; for PVL plate the Wlat—width of the lateral lamina, Wvent—width of the ventral lamina.

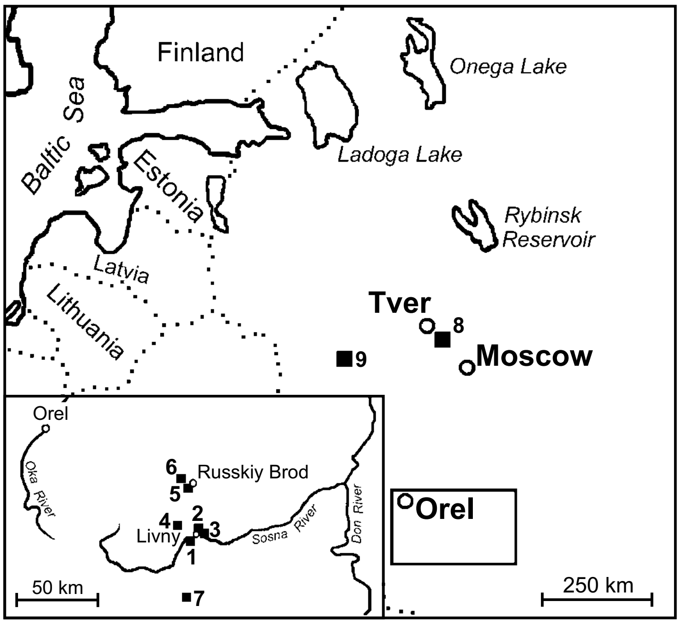

Fig. 1. Zadonskian antiarch localities in the Central European Russia. Orel Region: 1, Lime Factory quarry; 2, Kazatskiy quarry; 3, Livny town; 4, Shilivo village; 5, Russkiy Brod town; 6, Russkiy Brod quarry; 7, Zyabrovo village. Tver Region: 8, Redkino village; 9, Nelidovo village.

The antiarch collections from the Zadonskian Regional Stage are stored in the Palaeontological Institute of the Russian Academy of Sciences (PIN 1660, 2657, 3725).

Systematic palaeontology

Order Antiarchi Cope, 1885
Suborder Bothriolepidoidei Miles, 1968
Family Bothriolepididae Cope, 1886
Genus *Bothriolepis* Eichwald, 1840
Bothriolepis zadonica H.D. Obrucheva, 1983

Bothriolepis sp. nov. O.P. Obrucheva and H.D. Obrucheva 1977: 27. pl. 1: 1; H.D. Obrucheva 1980b: 95.
Bothriolepis sp. 1 H.D. Obrucheva 1980a: 42.
Bothriolepis sp. 2 H.D. Obrucheva 1980a: 42.
Bothriolepis zadonica H.D. Obrucheva 1983: 37–40, figs. 1, 2; Moloshnikov 2001a: 37; Moloshnikov 2001b: 32.

Holotype: Anterior median dorsal plate PIN 1660/3.

Diagnosis.—Large bothriolepidid placoderm, L of the head and trunk shields up to 40 cm. Flattened head shield hexagonal and wide and having straight rostral and lateral margins. Rostral margin of head shield wide. Upper infraorbital groove runs midway between lateral and orbital margins and one third of distance between rostral and orbital margins closer to rostral one. The preorbital recess of head shield very

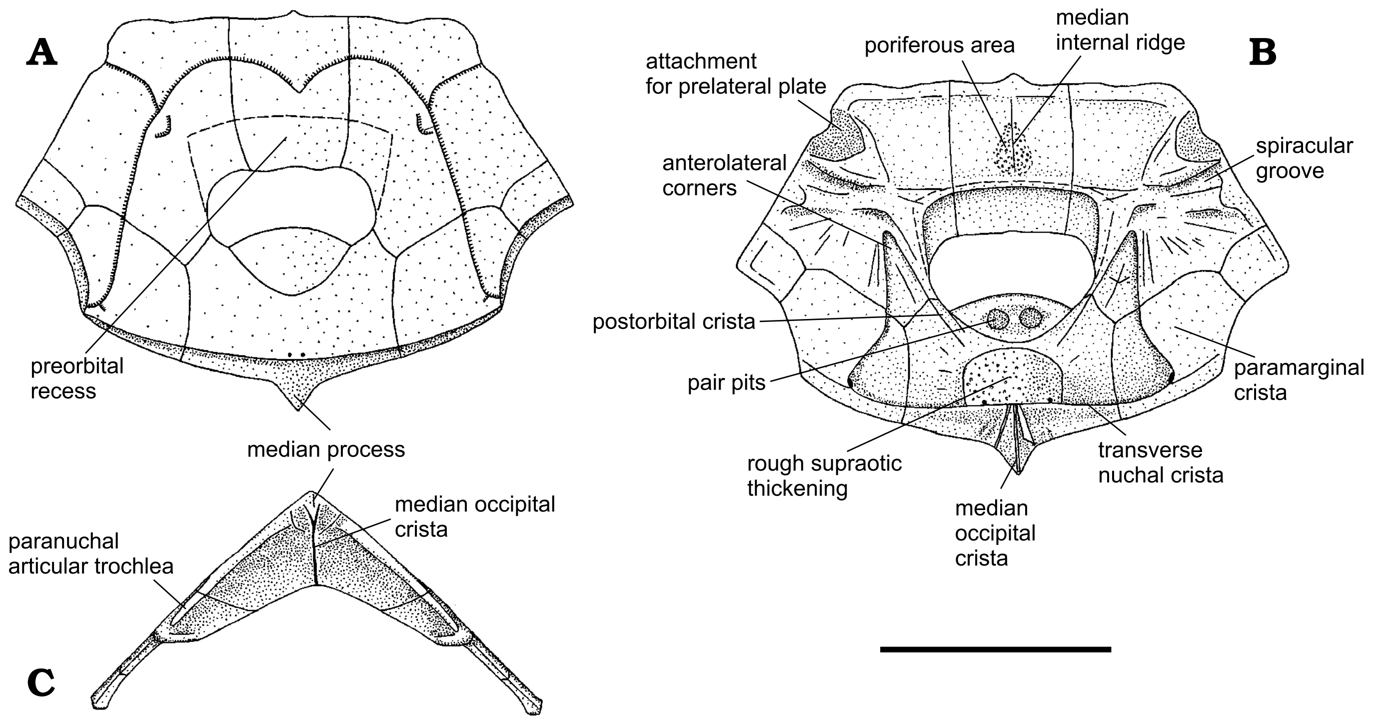

Fig. 2. Tentative restoration of *Bothriolepis zadonica* head shield; based on the isolated specimens PIN PrM 3725/100, PP 3725/1010, La 3725/1005, Nu 3725/1020 PNu 3725/87 and 3725/1094. Dorsal (**A**) and ventral (**B**) views of the flattened head shield. **C**. Posterior view of arched head shield. Scale bar 5 cm.

large and occupies almost up to the middle of premedian plate L. Angle between facial lamina and nasal one of premedian plate equals 60–80°. Preorbital recess of "trapezoid" type. Rough supraotic thickening of head shield very large, W of nuchal plate/W of supraotic thickening index equals about 2. Anterolateral corners of otico-occipital depression narrow at the base and only slightly expressed. Prespiracular (or lateral) pits at the internal surface of head shield absent. Trunk shield deep and narrow, with deep median dorsal crest. Anterior dorsolateral and mixilateral plates wide. Plates are ornamented by tubercles (adults), tubercles and ridges (subadults) or only ridges (juveniles). Lateral margin of pectoral appendages bears high tubercles.

Stratigraphical and geographic distributions.—Upper Devonian, Lower Famennian, Zadonskian Regional Stage, Central European Russia, Orel and Tver Regions.

Description

Large bothriolepidid placoderm, with the total L of the head and trunk shields up to 40 cm. The trunk shield bears the deep median dorsal crest.

Cranial skeleton

Head shield (Fig. 2).—Flattened head shield is wide, reaching maximum W between the posterolateral corners. The presumptive L/W (between the posterolateral corners) index in adult individuals equals 71. The head shield is convex in the cross section in the preorbital division and arched in the postorbital one. The arch angle ranges from 95° to 120°. The anterior and lateral margins of the head shield are straight. The posterior margin is convex. The orbital fenestra is rather small. The preorbital recess is very large and deep. The outline of this recess is unusual for bothriolepidids. Four types of preorbital recess are known in *Bothriolepis* species (Young 1988; Fig. 3): "simple" or "semicircular" of Long (1983), "trilobate", "pentagonal" and "trifid". The preorbital recess in *B. zadonica* does not fit these types. *B. zadonica* recess is characterised by development of two lateral corners, anterior and two lateral margins in its configuration (Fig. 2A). Here, this recess is named as "trapezoid" (Fig. 3C).

The premedian plate (*praemediale*, PrM) is narrow (Fig. 4B, F). The L/W1 index ranges from 119 to 140. One PrM plate (PIN 3725/1117) seems to be anomalous, in this specimen the L/W1 index is 97. However, other characteristics of this plate (type of the preorbital recess, presence of the poriferous area on the internal surface, position of the upper infraorbital groove and ornamentation) allow to refer it to *B. zadonica*. The anterior and posterior margins of the plate vary in shape from slightly concave, straight, to slightly convex. PIN 3725/100 bears median rostral corners on the anterior margin. Slightly expressed nasal notch is present in the two specimens (PIN 3725/100 and 1035). The anterior margin of the premedian plate is insignificantly longer than the posterior one. The W1/W2 index varies from 1.2 to 1.4; in the anomalous PrM plate, PIN 3725/1117, this index equals

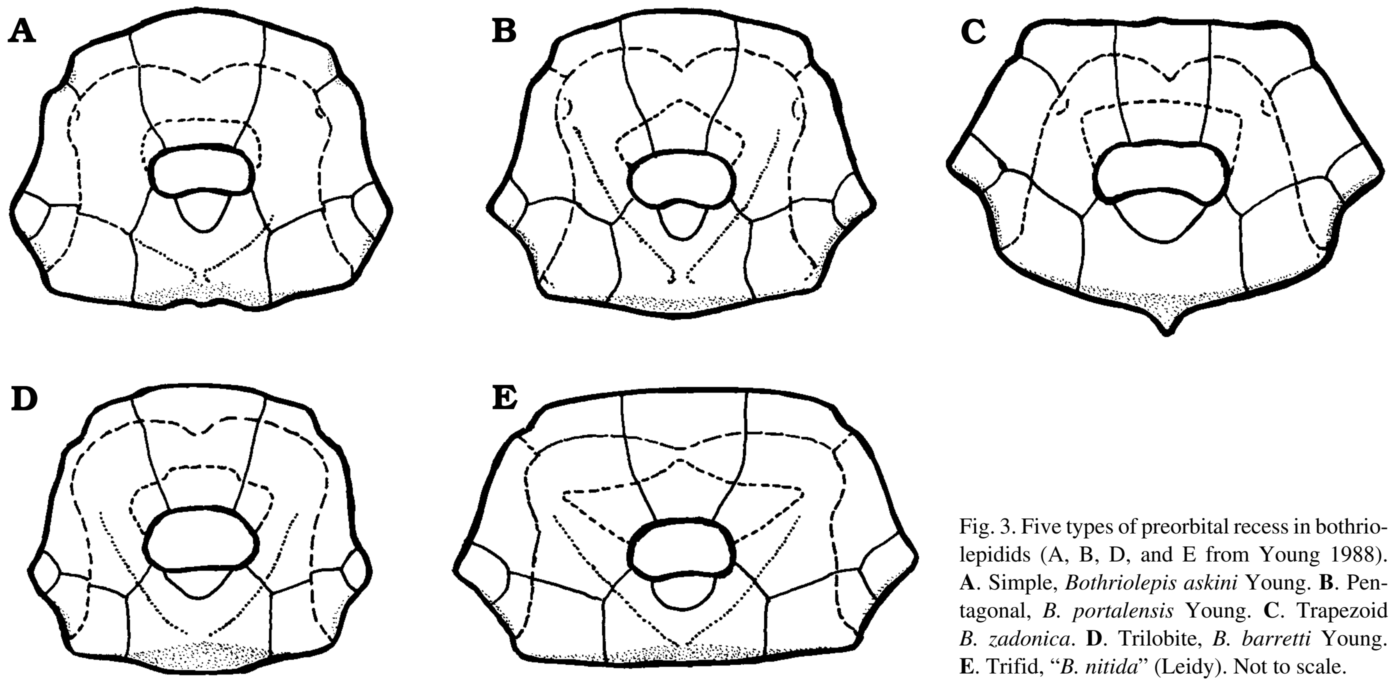

Fig. 3. Five types of preorbital recess in bothriolepidids (A, B, D, and E from Young 1988). **A**. Simple, *Bothriolepis askini* Young. **B**. Pentagonal, *B. portalensis* Young. **C**. Trapezoid *B. zadonica*. **D**. Trilobite, *B. barretti* Young. **E**. Trifid, "*B. nitida*" (Leidy). Not to scale.

1.7. The upper infraorbital groove is situated at the one third of the plate length from the anterior margin. The anterior median pit-line groove is distinct. The visceral surface is generally concave with developed poriferous area. The plate bears a low median ventral ridge. The posterior part of the PrM plate consists of two laminae (facial and nasal) which limit the very large preorbital recess. This recess occupies posterior half of the plate length. The anterior margin of the preorbital recess on all PrM plates (49) is straight and parallel to the rostral margin of the plate, and has no median corner in its configuration. The facial lamina is much thicker than the nasal one. The angle between these laminae equals 60–80°.

The lateral plate (*laterale*, L) is moderately wide (Fig. 4A). The L/W index in PIN 3725/1005 equals 110. The rostral margin is wide and straight. The lateral margin bears a small prelateral notch. The upper infraorbital groove runs between the lateral and orbital margins at a third of the distance from the rostral and orbital margins. The posterior oblique cephalic central pit-line groove disappears opposite to the middle of the orbital fenestra. The vertical pit-line groove is long. On the internal surface of the plate, the anterolateral corners of the otico-occipital depression are very narrow at the base and only slightly expressed. The spiracular groove is wide and distinct. The prespiracular (or lateral) pit is absent. The preorbital recess has one lateral corner in its configuration.

The postpineal plate (*postpineale*, PP). Its anterior margin is slightly or strongly convex and its posterior one is strongly convex (Fig. 4C). The L/W index ranges from 40 to 70. The paired pits are large and deep. They are situated in the centre or displaced towards the anterior margin.

The nuchal plate (*nuchale*, Nu) is arched. The arch angle ranges from 95 to 120°. The plate is wide (Figs. 4E, 5), its L1/W1 index equals 50–90. The W is largest between the lateral and posterolateral corners. The anterolateral margins are straight and 2–3 times shorter than the posterolateral ones. The shape of the posterior margin ranges from slightly concave to slightly convex. The posterior margin of this plate bears the large median process. The nuchal area passes onto the paranuchal plates. The posterior oblique cephalic central pit-line groove is present only in juveniles and subadults. The distance between the internal endolymphatic duct openings is 3–4 times larger than between the external ones. The very large rough supraotic thickening is situated at the internal surface of the nuchal plate in its central part. The W of Nu/W of this supraotic thickening index equals 2. This index equals about 4 in specimens of *Bothriolepis canadensis* (Stensiö 1948) and in specimens of *B. yeungae* (Johanson 1998). The postorbital crests are only slightly expressed. The transverse nuchal crest is very high and continues onto the paranuchal plates. The area posterior to the transverse nuchal crest is long and bears high median occipital crest and two low additional crests asymmetrically located to the sides from the occipital crest.

The paranuchal (*paranuchale*, PNu) plate is wide (Fig. 4D, G). L/W index ranges from 70 to 100. The narrow obtected nuchal area is situated along the posterior margin. It reaches the posterolateral corners of the head shield. The paramarginal crest is situated at the visceral surface. The posterolateral corners of the otico-occipital depression are rounded. The posterior part of the PNu is thick. It bears the paranuchal articular trochlea.

Postmarginal plate (*postmarginale*, PMg) is tetragonal (Fig. 4D). L/W index equals about 100. The anterior margin is convex, the median one is straight and the lateral one is straight and short.

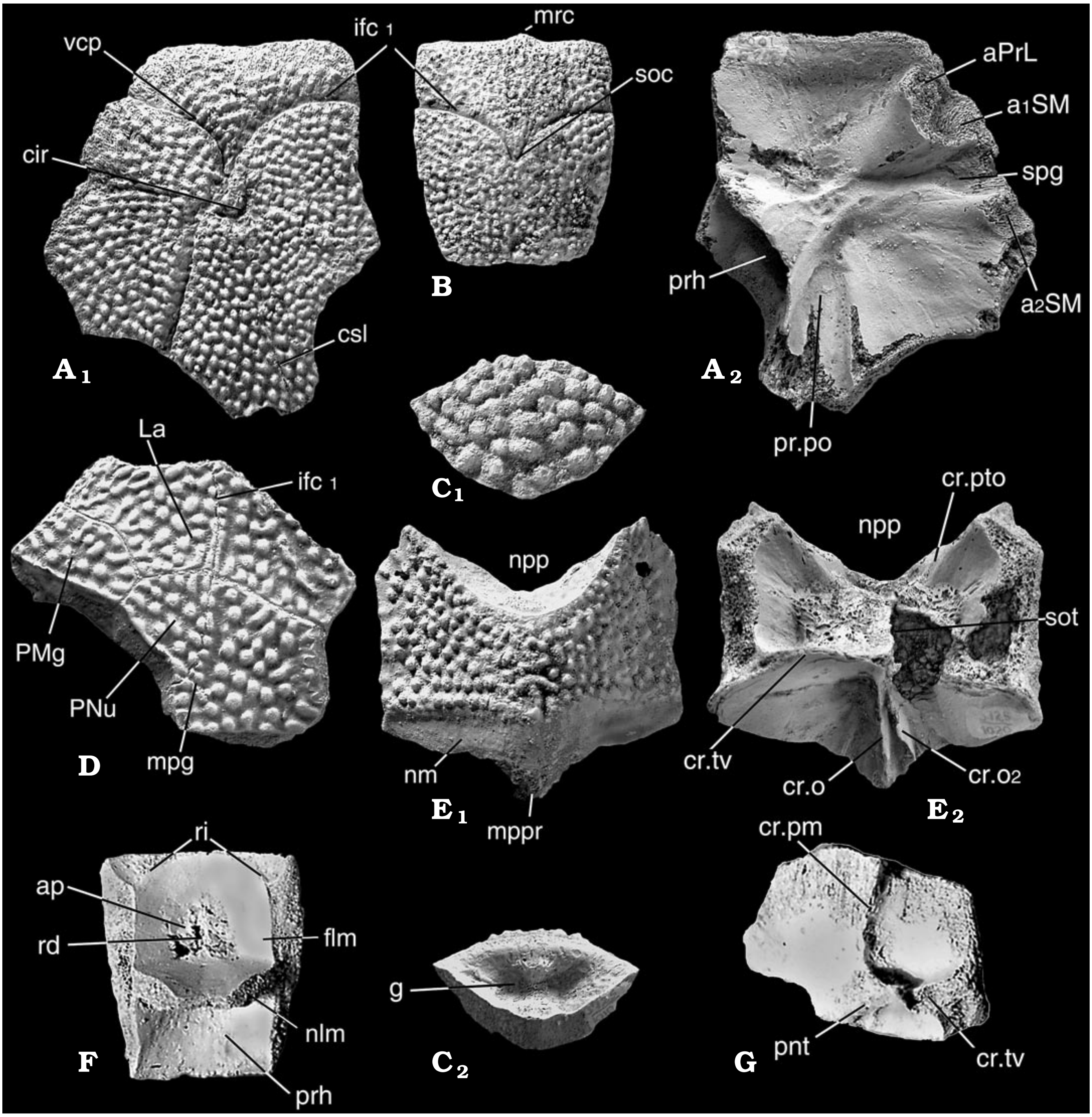

Fig. 4. Head shield plates of *Bothriolepis zadonica*. **A**. Left lateral, PIN 3725/1005 in dorsal (A_1) and ventral (A_2) views, × 1.15. **B**. Premedian, PIN 3725/100, dorsal view, × 1.1. **C**. Postpineal, PIN 3725/1010 in dorsal (C_1) and ventral (C_2) views, × 1.3. **D**. Left lateral, paranuchal and postmarginal in articulation, PIN 3725/1094, dorsal view, × 1.5. **E**. Nuchal, PIN 3725/1020, dorsal (E_1) and ventral (E_2) views, × 1. **F**. Premedian, PIN 3725/1132, ventral view, × 1.1. **G**. Right paranuchal, PIN 3725/87, dorsal view, × 1. Abbreviations: a1SM and a2SM, anterior and posterior attachment on lateral plate for submarginal plate; ap, poriferous area of premedian plate; aPrL, attachment on lateral plate for prelateral plate; cir, semicircular pit-line groove; cr.o, median occipital crest; cr.o2, additional occipital crest; cr.pm, paramarginal crest; cr.pto, postorbital crest; cr.tv, transverse nuchal crest of the head shield; csl, central sensory pit-line groove; flm, facial lamina; g, pair pits on postpineal plate; ifc1, upper infraorbital groove; La, lateral plate; mpg, middle pit-line groove; mppr, median process on the nuchal plate; mrc, median rostral corner of the premedian plate; nlm, nasal lamina; nm, obtected nuchal area; npp, postpineal notch of the nuchal plate; PMg, postmarginal plate; pnt, paranuchal articular trochlea; PNu, paranuchal plate; prh, preorbital recess of head shield; pr.po, anterolateral corners of otico-occipital depression; rd, median internal ridge on the premedian plate; ri, oblique premedian ridge; soc, anterior median pit-line groove; sot, rough supraotic thickening of nuchal plate; spg, spiracular groove; vcp, vertical pit-line groove.

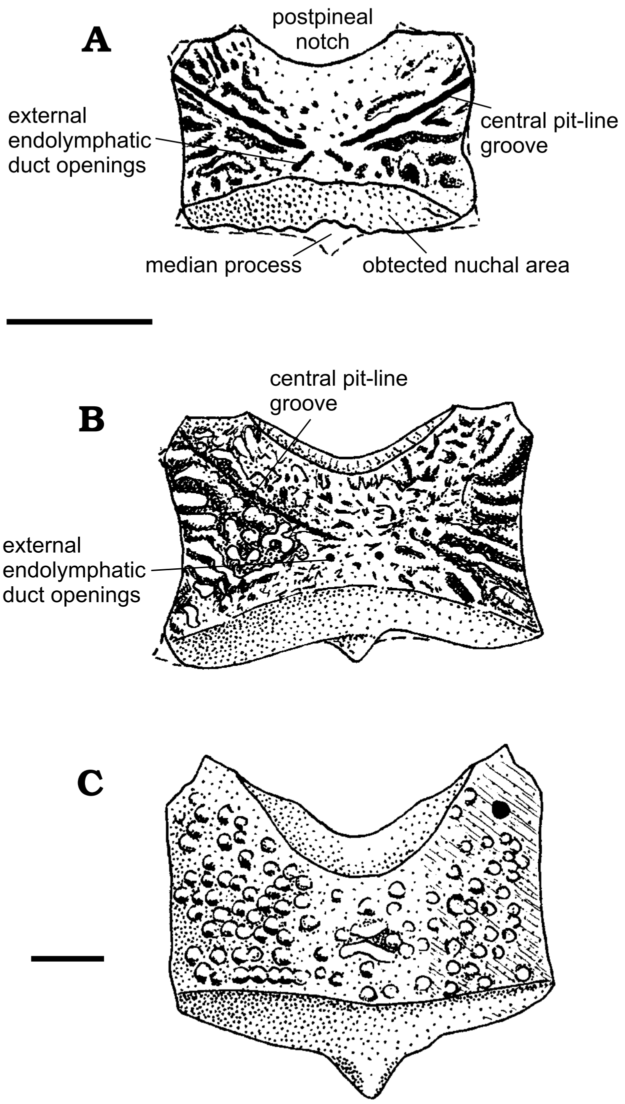

Fig. 5. Three nuchal plates of *Bothriolepis zadonica*. **A**. Juvenile, PIN 3725/23. **B**. Subadult, PIN 3725/24. **C**. Adult, PIN 3725/1020. Scale bars 1 cm.

Submarginal plate (*submarginale*, SM). There is only one submarginal plate PIN 3725/1185 in the collection (Fig. 6A). This plate is short, low anteriorly and high posteriorly.

Jaw elements. There is one large S-shaped inferognathal plate (*inferognathale*, Ifg; PIN 3725/1118; Fig. 6B) in the collection of the Zadonskian antiarch. This plate is wide and short. The L of the anterior (biting) division / L of the posterior (non-biting) division index equals 62. The groove of the Meckelian cartilage is wide and shallow. The labial surface of the anterior division is ornamented with short branching grooves.

It is very interesting that the structure of the superficial bone layer is different in the two inferognathal divisions: the biting division shows a porous superficial bone layer, and also bears short branching grooves, like in turtle jaws. The jaws of turtles are covered with a horny sheath forming the biting surface of the beak. In modern agnathans and fishes horny structures are also well known, for example, toothlike structures of the petromyzontiforms and cyprinids. It is suggested, therefore, that the jaws of the antiarchs (bothriolepidids) might also have been covered with keratinous biting surface.

Postcranial skeleton

Trunk shield (Figs. 7–9).—The reconstructed trunk shield is narrow and deep. The L of the ventral wall exceeds the L of the dorsal one. The dorsal wall is arched and ventral one is flat. The arch angle of the dorsal wall equals 90–120°. The very deep dorsal median crest is situated on the dorsal wall (Figs. 7C, 9). Its depth equals 25% of the total trunk shield depth.

The anterior median dorsal (*anterior medio-dorsale*, AMD) plate is moderately wide (Figs. 7A, C, 8A), its L/W index equals 70–90. The plate is arched. The angle between the right and left sides of the anterior median dorsal plate is 85–120°. In PIN 1160/3 the anterior division is arched and the posterior division is flat. The anterior margin of this plate is convex. Its W is 1.5–2 times less than the total W and

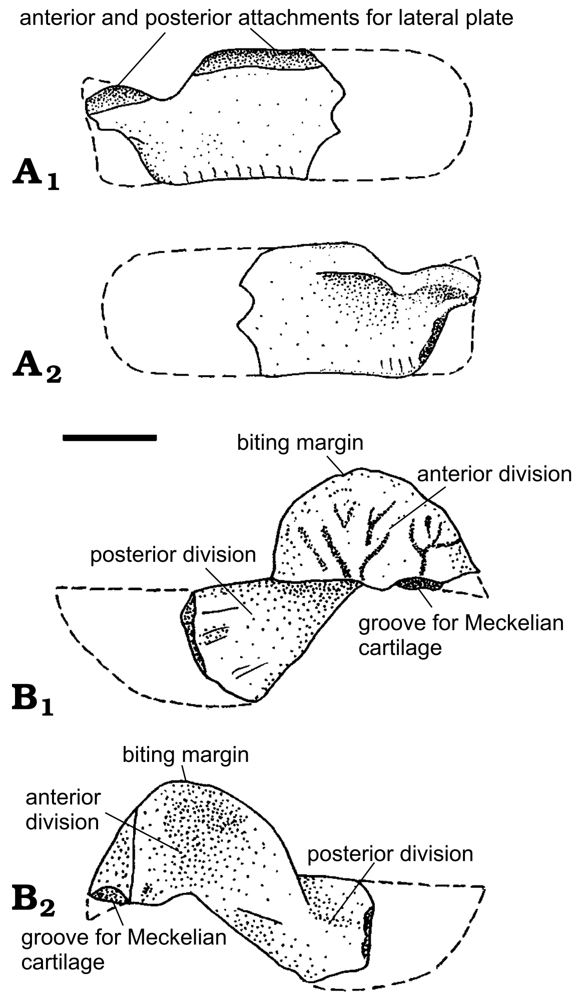

Fig. 6. *Bothriolepis zadonica*. **A**. Left submarginal plate, PIN 3725/1185 in external (A_1) and internal (A_2) views. **B**. Left inferognathal plate, PIN 3725/1118, labial (B_1) and lingual (B_2) surfaces. Scale bar 1 cm.

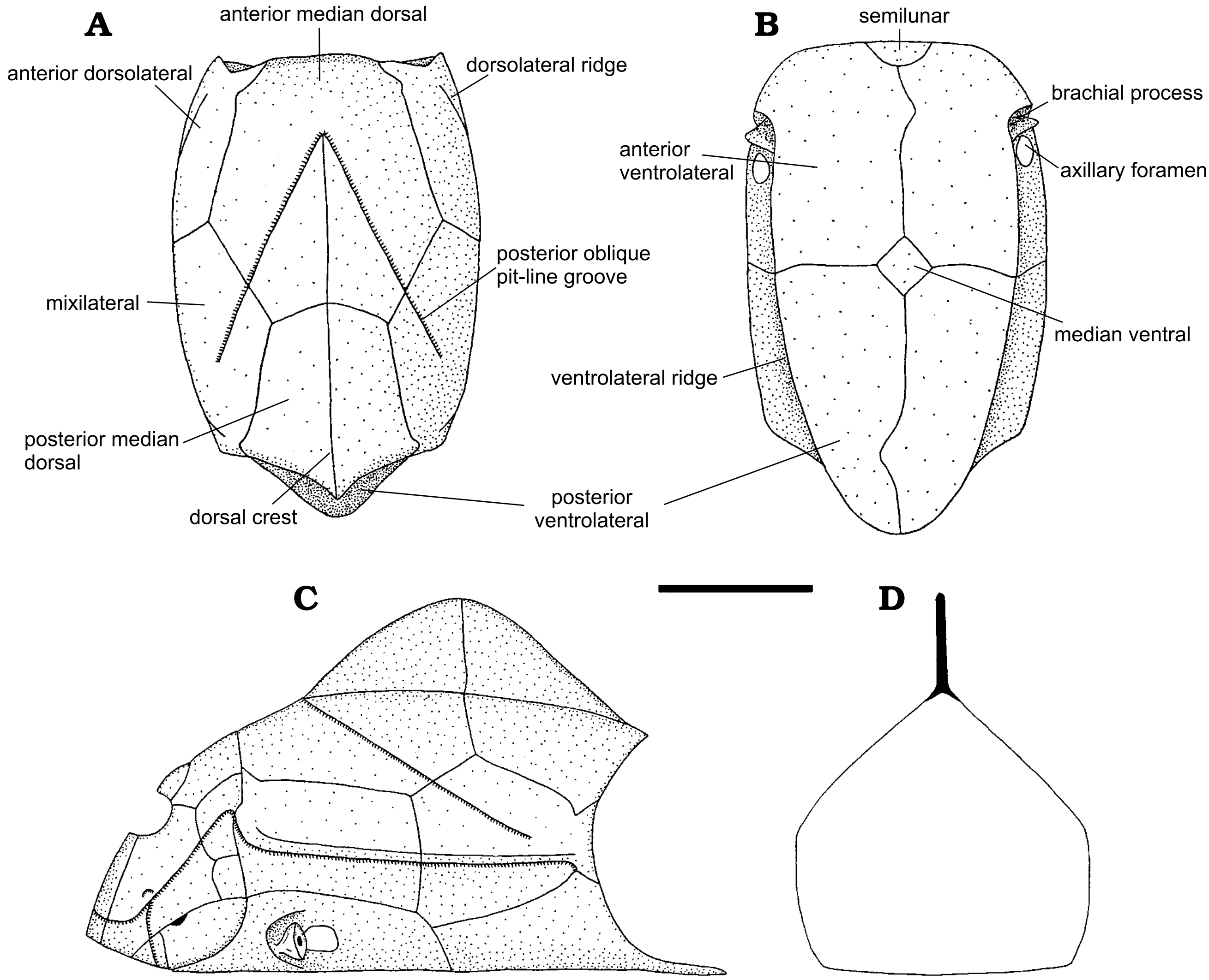

Fig. 7. Tentative restoration of *Bothriolepis zadonica* H.Obr. trunk shield; based on the isolated specimens PIN AMD 1660/19, PMD 3725/63, ADL 3725/65, MxL 3725/63, AVL 3725/46, PVL 1660/9. Dorsal (**A**) and ventral (**B**) views. **C**. Head and trunk shields in left lateral view. **D**. Cross section of the trunk shield at the suture between anterior and posterior median dorsal plates. Scale bar 10 cm.

slightly larger or equals the W of the posterior margin. The L of the anterior division of the AMD plate is 1.3–1.5 times greater than the L of the posterior one. The tergal angle is situated at the distance of one third of the plate length from the anterior margin. However, in one specimen (PIN 1660/18) the tergal angle is situated at the one quarter of the plate L from the anterior margin. The very deep dorsal median crest originates from the tergal angle. It attains its maximum depth at the suture between the AMD and PMD plates. The anterior oblique abdominal pit-line groove is absent and the posterior one is distinct and passes to the MxL plate (PIN 1660/3, 16) or to the PMD plate (PIN 1660/18). The latter position of the posterior oblique abdominal pit-line groove is anomalous among bothriolepidids. The remigolepidid type of suture is present at the left side of the holotype (PIN 1660/3): in its anterior part the AMD plate overlapped the MxL and in its posterior part on the contrary—the MxL overlapped the AMD plate. The levator fossa is distinct and deep; it is limited by the deep postlevator crests. The median ventral ridge of the levator fossa is distinct. The anterior ventral pit is situated below the tergal angle. It is deep and narrow. The median ventral ridge on the internal surface of this plate is low, it originates from the middle of the plate length (PIN 1660/3, 18) or from the anterior ventral pit (PIN 1660/19). The median ventral ridge passes into the short ventral median groove in the posterior part of the plate.

The posterior median dorsal plate (*posterior mediodorsale*, PMD) is narrow and arched (Figs. 7A, C, 8B, C, D). The arch angle (between the posterolateral corners) equals 85–120°. The anterior and posterior margins are convex. The posterior margin of the plate is 1.5 times shorter than the anterior one. The posterior oblique abdominal pit-line groove runs from the AMD plate in all the specimens. In PIN 3725/63 the asymmetry is present at the arrangement of the right and left lines of this groove. The ventral median ridge is present at the internal surface only in the specimen PIN

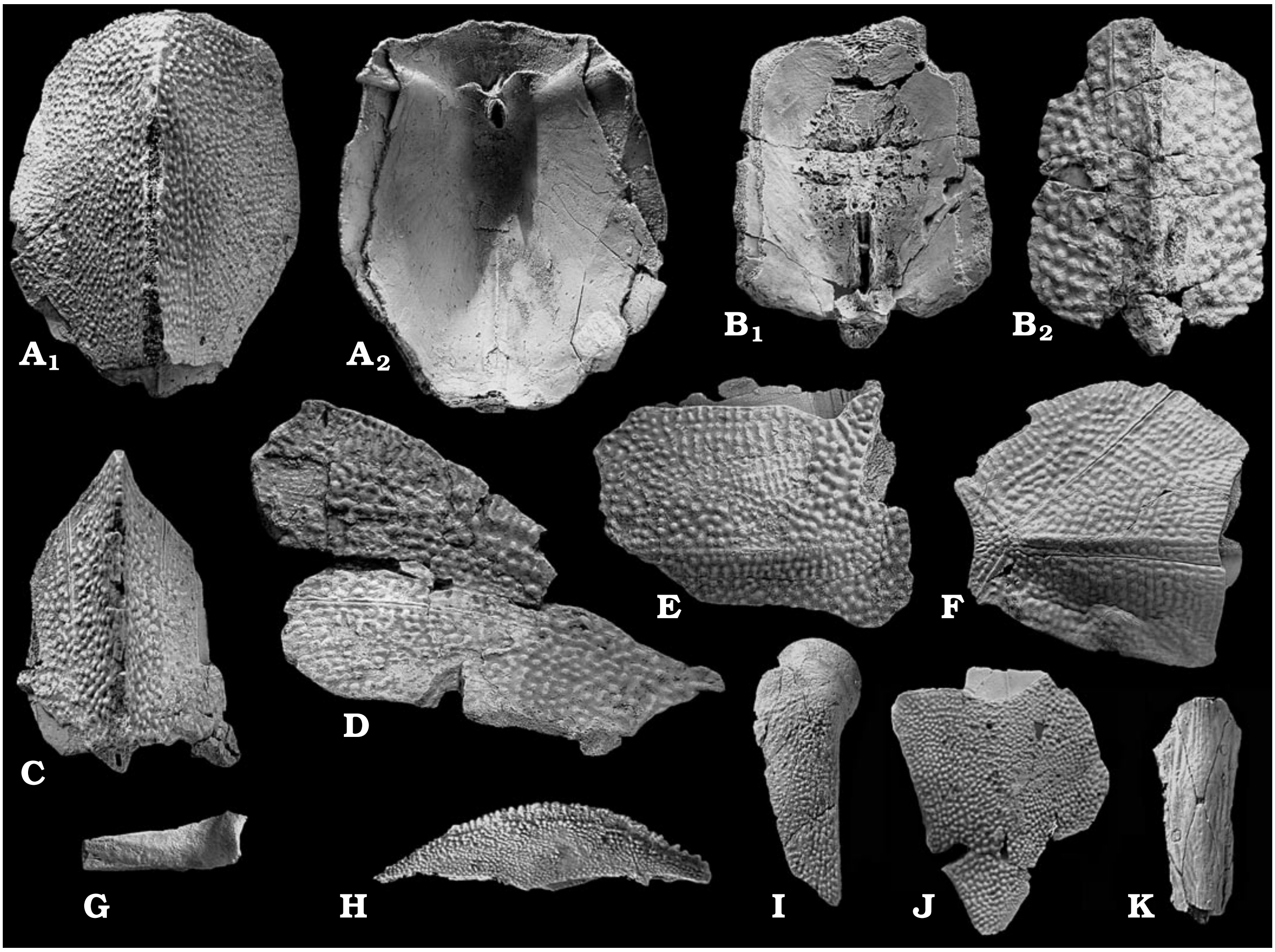

Fig. 8. Trunk shield plates of *Bothriolepis zadonica*. **A**. Anterior median dorsal, PIN 1660/18 in dorsal (A_1) and ventral (A_2) views, × 0.65. **B**. Posterior median dorsal, PIN 3725/63 in ventral (B_1) and dorsal (B_2) views, × 0.6. **C**. Posterior median dorsal, PIN 1660/10 in dorsal view, × 0.75. **D**. Posterior median dorsal, PIN 3725/1115 in left lateral view, × 0.4. **E**. Right anterior dorsolateral, PIN 3725/65 in external view, × 0.8. **F**. Right mixilateral, PIN 3725/68 in external view, × 0.4. **G**. First mesial marginal plate of the right pectoral appendage, PIN 3725/1072 in external view, × 0.6. **H**. Second lateral marginal plate of the right pectoral appendage, PIN 3725/1016, × 1. **I**. First ventral central of the right pectoral appendage, PIN 3725/1011 in external view, × 0.65. **J**. Right posterior ventrolateral, PIN 1660/9 in external view, × 0.4. **K**. Distal segment of pectoral appendage, PIN 3725/1016, × 1.5

3725/1115. The posterior ventral pit is deep, long and narrow. The *crista transversalis interna posterior* is smooth and the area posterior to this crista is short.

The anterior dorsolateral plate (*anterior dorso-laterale*, ADL) is wide and short (Figs. 7A, C, 8E). The L of the dorsal and lateral laminae is 2.5 times greater than their W. The Wdors equals the Wlat. The lateral and dorsal laminae converge at the angle of 130–150°. The dorsolateral ridge is gentle; it is distinct only in PIN 1660/22. The postnuchal ornament corner is sharp, long and narrow. The main lateral line groove is distinct.

The mixilateral (*mixilaterale*, MxL) plate is wide and short (Figs. 7A, C, 8F). The dorsal lamina is twice wider than the lateral one. The L of the lateral lamina exceeds its W almost twice. The L of the dorsal lamina is 1.5 times greater than its W. The angle between the dorsal and lateral laminae equals 140–160°. The smooth dorsolateral ridge is present in the posterior parts of the MxL plate. The posteroventral ornamental corner is wide. The posterior oblique abdominal pitline groove is distinct and does not reach the lateral margin. The main lateral line groove is distinct.

The anterior ventrolateral (*anterior ventro-laterale*, AVL) plate (Fig. 7B, C), the brachial processes and fragments of the ventral and lateral laminae are present in the collection. The lateral lamina is perforated with the rather rounded large axillary foramen. The angle between the lateral and ventral laminae equals approximately 120°.

The posterior ventrolateral plate (*posterior ventrolaterale*, PVL) is moderately wide (Figs. 7B, C, 8J). There is only one complete plate, which is a left PVL (PIN 1660/9), in the collection. The L of the ventral lamina is 1.3 times greater than its W. The lateral lamina is low. The W of the ventral

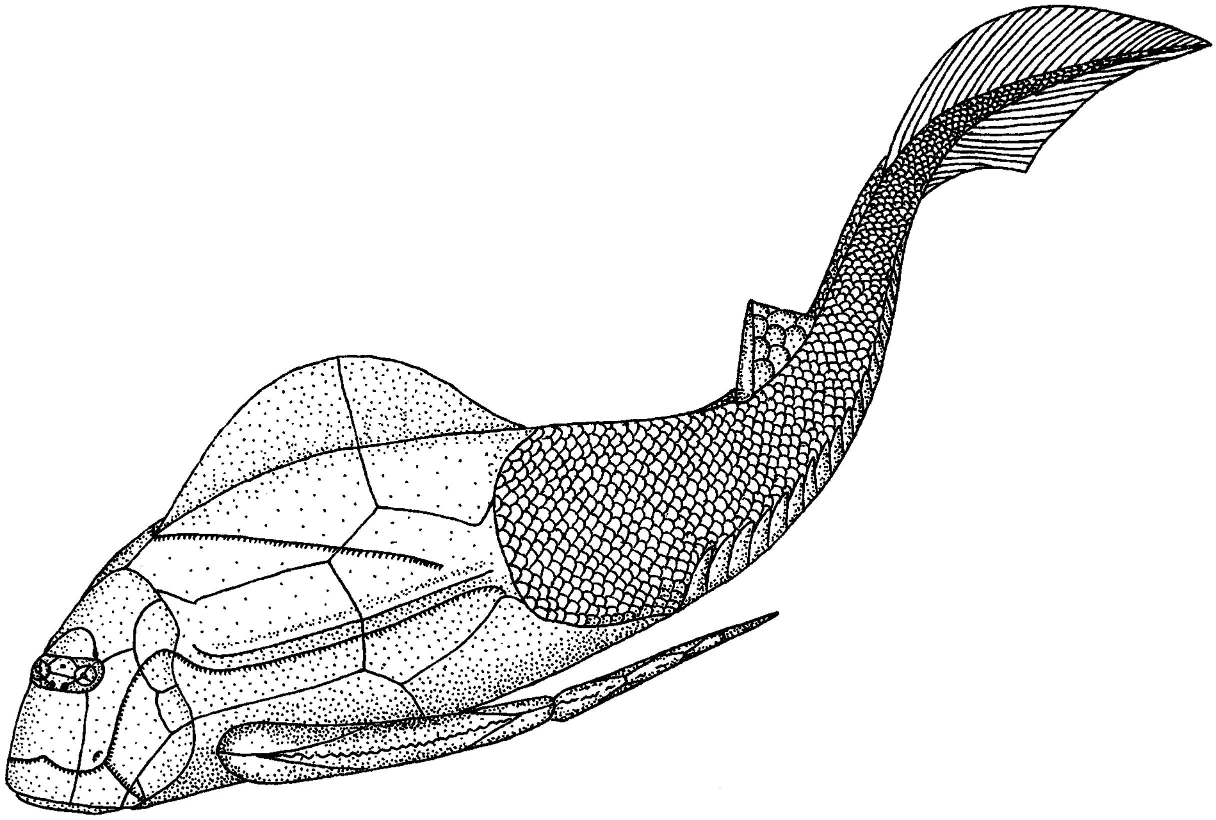

Fig. 9. Tentative restoration of *Bothriolepis zadonica*; caudal fin morphology from *Bothriolepis gippslandiensis* (based on Long and Werdelin 1986).

lamina is 1.1 times greater than the W of the lateral one. The angle between the lateral and ventral laminae equals about 140°. The ventrolateral ridge is gentle. The left PVL plate overlapped the right one.

Plates of the pectoral appendages.—The proximal segment of the pectoral appendage armour is ornamented with tubercles or tubercles and ridges. The distal segment bears low longitudinal ridges (PIN 3725/57, 1016 and others; Fig. 8K). The first ventral central plate (*centrale-ventrale 1*, Cv 1; PIN 3725/1011) is narrow and long (Fig. 8I), its L/W index equals 300. The second lateral marginal plate (*marginale-laterale 2*, Ml 2; PIN 3725/1015) is narrow (Fig. 8H), its L/W index equals 360. The first mesial marginal plate (*marginale-mediale 1*, Mm 1; PIN 3725/1070, 371072) is smooth (Fig. 8G).

Ornamentation.—The plates of the juvenile individuals are ornamented with ridges or tubercles and ridges, in adults with high tubercles only.

Ontogenetic and individual variations

Ontogenetic variations.—The ontogenetic variations in *Bothriolepis zadonica* are expressed in disappearance of the seismosensory pit-line groove from the external surface of the plates, and in changes of the plate ornamentation.

Disappearance of the seismosensory pit-line grooves from the plates.—The posterior oblique cephalic central pit-line groove is situated at the Nu plate only in juvenile individuals of *B. zadonica* (L of the head and trunk shields about 12–15 cm; Fig. 5A, B). In adult and subadults individuals (L of the head and trunk shields about 20–40 cm; Fig. 5C) this pit-line groove is absent. Such lack of the seismosensory pit-line grooves from the plates is known in many *Bothriolepis*-species, for example, *B. canadensis*, *B. prima*, *B. obrutschewi,* and *B. ciecere* (Stensiö, 1948; Karatajute-Talimaa, 1966; Lukševičs, 1991).

Change of the external ornamentation.—The plates of the juvenile individuals (L of the head and trunk shields about 12–15 cm) in *B. zadonica* bear ridged sculpturing (Nu: PIN 3725/23, 1025; Fig. 5A). The plates of the subadult individuals (L of the head and trunk shields about 15–25 cm) are tuberculated and ridged (Nu: PIN 3725/24 and PP: PIN 3725/14, 15; Fig. 5B). In adult individuals (L of the head and trunk shields about 30–40 cm) the plate ornamentation consists of tubercles (Nu: PIN 1660/4 and PP: PIN 3725/1010, 1012; Figs. 4A–E; 5C). Thus, the plate surface in the juvenile individuals was ridged and during ontogeny the ridge junctions thickened and gave rise to tubercles.

Individual variation.—The individual variation in *B. zadonica* is expressed by: (1) character of passage of the seismosensory grooves at the plates, (2) character of the trunk shield plates overlap, (3) median angles between the right and left sides of the AMD and PMD plates, (4) angle between the dorsal and lateral laminae of the ADL and MxL plates, (5) position of the tergal angle in the AMD plate, (6) changes in the shape of the head shield plates.

Character of the passage of the seismosensory grooves.—The posterior oblique abdominal pit-line groove passes in bothriolepidids normally from the AMD to the MxL plate. The normal arrangement of this pit-line groove in *B. zadonica* is present in the specimens AMD PIN 1660/3 and 19, and MxL PIN 3725/68 and 1121 (Fig. 8F). In the specimens AMD PIN 3725/69 and 1660/18 the posterior oblique abdominal pit-line groove passes almost in parallel to the dorsal crest and to the PMD plate (Fig. 8A_1, B_2, C, D). The right and left lines of this groove are normally arranged symmetrically in bothriolepidids. The asymmetry in the arrangement of these pit-line grooves is present in the specimen PMD PIN 3725/63 (Fig. 8B_2). The distance between the right line and the dorsal crest is 1.5 times greater the distance between the crest and the left one.

Character of the trunk shield plates overlap.—In bothriolepidids the AMD and PMD plates are normally blocked by the MxL plate. The normal overlap of the trunk shield plates in *B. zadonica* is present in the MxL (PIN 3725/1121) and AMD (PIN 1660/19) plates. In the specimen AMD PIN 1660/18 the MxL plate is blocked by this AMD plate. The anomalous remigolepidid suture is present in the holotype (PIN 1660/3) at the left side of this AMD plate (H.D. Obrucheva 1983: fig. 2a). The AMD plate overlaps the MxL plate in the anterior division and in posterior division the situation is in the contrary: MxL overlaps the AMD. For example, anomalous character of the overlap is also seen in some specimens of the *B. canadensis* and *B. ciecere* (Stensiö 1948; Lukševičs 1991).

Median angles between the right and left sides of the AMD and the PMD plates.—The angle between the right and left sides of the AMD and PMD plates in *B. zadonica* equals 85°–120°. The angle between the right and left sides of the AMD plate at the anterolateral corners in the specimen PIN 1660/18 equals 85°, in the PIN 1660/19—90° and in the PIN 1660/3—120°. The angle between the right and left sides of the PMD plate in its anterior division in the specimen PIN 3725/1115 equals 85°, in the PIN 1660/10—90° and in the PIN 3725/63—120°.

Angle between the dorsal and lateral laminae of the ADL and the MxL plates. In the specimen ADL PIN 1660/22 the angle between the dorsal and lateral laminae equals 125°, in the ADL PIN 3725/65—150°. The variability in the angles between the dorsal and lateral laminae of the ADL and MxL plates exists in many bothriolepidids.

Position of the tergal angle.—The tergal angle is situated at the one third of the AMD plate length from its anterior margin. In the AMD plate (PIN 1660/18) it is placed at the one quarter of the plate length from the anterior margin.

Variation in the shape of the head shield plates.—The individual variabilities of the plate shape in *B. zadonica* are insignificant. The posterior margin of the Nu plate is concave (PIN 1660/4) or convex (PIN 3725/1020). For example, the variation of the posterior margin of the Nu plate is present in *B. ciecere* and in *B. volongensis* (Lukševičs 1991; Lukševičs and Sorokin 1999).

The difference in configuration of the posterior and anterior margins of the PP plate is also present. In PIN 3725/1012, as opposed to other specimens, the posterior margin is strongly convex. The anterior margin of the PP plate is strongly convex in PIN 3725/12 and in the other specimens it is slightly convex or almost straight.

The W1 of the PrM plate almost equals the W2 in all PrM plates in our collection. In the specimen PIN 3725/1117 the W1 is 1.7 greater than the W2 (see description of the PrM plate).

Measurements of some specimens, mm.—PrM. 3725/100: L = 337; W1 = 28.2; W2 = 21.3. 3725/1035: L = 27.6; W1 = 21.7; W2 = 15.3. 3725/1034: L = 25.75; W1 = 19.5; W2 = 15.15. 3725/1033: L = 24.8; W1 = 19.75; W2 = 12. 3725/1130: L = 33.2; W1 = 28.7; W2 = 19.3. 3725/1132: L = 28.8; W1 = 24.4; W2 = 18.6. 3725/1131: L = 31.8; W1 = 25.6; W2 = 16.6. 3725/1133: L = 22.15; W1 = 19; W2 = 13.25. 3725/1138: L = 24; W1 = 21; W2 = 14.2. 3725/1117: L = 35; W1 = 36; W2 = 21.

La. 3725/1005: L = 47.5; W = 44.3.

PP. 3725/1043: L = 19.7; W = 28.2. 3725/1045: L = 11.2; W = 15.7. 3725/1047: L = 13.7; W = 20. 3725/1046: L = 12.75; W = 18.2. 3725/1012: L = 21.8; W = 31.5. 3725/1010: L = 18; W = 30.2. 3725/15: L = 11.2; W = 17.5. 3725/13: L = 15.6; W = 25. 3725/12: L = 20; W = 28. 3725/1158: L = 16; W = 22. 3725/1159: L = 8.75; W = 15.8. 1660/6: L = 21.8; W = 30.

Nu. 3725/1020: L1 = 47.1; L2 = 32.8; W1 = 52.9; W2 = 52. 3725/24: L1 = 20.3; L2 = 17; W1 = 28; W2 = 27.4. 3725/23: L1 = 13.35; L2 = 12; W1 = 19.4; W2 = 19.8. 3725/1162: L1 = 23.5; L2 = 17.6; W1 = 30; W2 = 27.8. 3725/1160: L1 = 27.5; L2 = 23; W1 = 36.8; W2 = 37.5. 1660/4: L1 = 29; L2 = 22; W1 = 41; W2 = 43.

PNu. 3725/87: L = 31.9; W = 41.2. 3725/86: L = 25.2; W = 32.5. 3725/43: L = 25; W = 35.2. 3725/38: L = 17.1; W = 20.5. 3725/41: L = 16.2; W = 20.9. 3725/1107: L = 29.3; W = 33.6. 3725/1174: L = 21.75; W = 29.65. 3725/1176: L = 24.6; W = 32.75. 3725/1175: L = 16.6; W = 21.4. 3725/1173: L = 24; W = 32.5.

PMg. 3725/1156: L = 17.5; W = 17.2. 3725/1153: L = 16.4; W = 16. 3725/1154: L = 14.5; W = 15. 3725/1157: L = 13.4; W = 12.62.

AMD. 1660/19: L = 137.4; W = 152.4. 1660/18: L = 77; W = 101. 1660/3, holotype: L = 145; W = 161.

PVL. 1660/9: L = 86; Wvent = 46.2; Wlat = 39.8.

MxL. 3725/68: L = 112; Wdors = 66.3; Wlat = 51.

Comparison with other crested species.—*B. zadonica* strongly differs from all *Bothriolepis* species known from the Devonian of Russia by the larger size of the armour, arched Nu, AMD and PMD, presence of the deep dorsal crest, larger rough supraotic thickening of the head shield and preorbital recess, type of this recess and tubercular ornamentation of the plates. Among bothriolepidids from Russia, also *B. heckeri* Lukševičs, 2001 has a dorsal crest; *B. zadonica* differs from it by the larger size, deeper dorsal crest, proportions of the head shield plates and AMD, and larger arched angle of this plate. Among the bothriolepidids from Scotland, *B. zadonica* is close to *B. cristata* Traquair, 1895, which also has a dorsal crest (Miles 1968). However, it strongly differs from the latter by the larger size of the armour, narrower AMD and wider ADL and MxL, absence of the anterior oblique abdominal pit-line groove. The crested bothriolepidids are also known from Victoria, Australia (Long 1983; Long and Werdelin 1986). *B. zadonica* differs from *B. gippslandiensis* Hills by larger size of the armour, presence of the well developed median process of the Nu, absence of the prespiracular (lateral) pits on the internal surface of the L, larger preorbital recess, longer AMD and PMD, proportions of the ADL and MxL, presence of the isolated tubercles on the lateral margin of the pectoral appendages. *B. zadonica* differs from *B. cullodenensis* Long by larger size of the armour, presumable smaller orbital fenestra of the head shield, wider head shield, absence of the prespiracular (lateral) pits, larger preorbital recess of the head shield and type of this recess, proportions of the AMD and PMD, ADL and MxL, absence of the oblique transverse ridges on the external surface of the AMD, presence of the isolated tubercles on the lateral margin of the pectoral appendages. *B. zadonica* differs from *B. fergusoni* Long by deeper median dorsal crest, wider Nu and PNu, absence of the prespiracular pits, proportions of the AMD and PMD (*B. zadonica* has narrower anterior division of the AMD), absence of the oblique transverse ridges on the external surface of the AMD, presence of the isolated tubercles on the lateral margin of the pectoral appendages.

Conclusion

Bothriolepidid placoderms are also of interest palaeozoogeographically. Young (1981, 1993) discussed the problems of the vertebrate palaeozoogeography and identified five separated faunal provinces in the Late Devonian. The crested bothriolepidid antiarchs are known only from two provinces: Euramerica (*B. zadonica* and *B. heckeri*) and East Gondwana (*B. gippslandiensis*, *B. cullodenensis*, and *B. fergusoni*). However, Young suggested that the Famennian faunas of the East Gondwana province are characterised by close similarity to Euramerica in their vertebrate elements (Young 1993: 304). That means a close relationship between these two provinces in the Late Frasnian or in the Early Famennian, during which the exchanges of the placoderm elements took place. The crested *Bothriolepis* species are known from the lower and middle part of the Frasnian of the Australia, East Gondwana (Long and Werdelin 1986), and from the Famennian of Russia, Euramerica. These facts allow to come to two conclusions on the evolution of the crested bothriolepidids. First, the origin of the Famennian Euramerican crested bothriolepidids was related to the influence of the Frasnian crested bothriolepidids from the East Gondwana, and the Euramerican crested bothriolepidids are descendants of the Gondwanian forms. Second, the presence of the median dorsal crest is a parallelism in the evolution of the bothriolepidids, and is a similar adaptation to the aquatic environment, and the origin of this adaptation in the bothriolepidids of these two separated provinces was not related.

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