Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform

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ABSTRACT
A large collection of bothriolepid antiarch material from 26 localities in the north-western part of the East European Platform (Latvia, Lithuania, and the Leningrad, Novgorod, and Pskov regions of Russia) is described and illustrated, with a critical treatment of previously described material. The genus *Grossilepis* Stensiö, 1948 is represented by two species, *Grossilepis tuberculata* (Gross, 1941) and *G. spinosa* (Gross, 1942). All remaining material is referred to the genus *Bothriolepis* Eichwald, 1840: *B. prima* Gross, 1942, *B. obrutschewi* Gross, 1942, *B. cellulosa* (Pander *in* Keyserling, 1846), *B. panderi* Lahusen, 1880, *B. traudscholdi* Jaekel, 1927, *B. maxima* Gross, 1933, *B. evaldi* Lyarskaja, 1986 come from the Givetian(?)-Frasnian deposits, and *B. leptocheira curonica* Gross, 1942, *B. ornata* Eichwald, 1840, *B. jani* Lukševičs, 1986, *B. heckeri* n. sp., *B. ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974 as well as one unnamed form come from the Famennian sequence. The stratigraphic distribution of bothriolepids through the Middle/Upper Devonian of the Main Devonian Field is clarified in a proposed new version of the vertebrate zonation. A cladistic analysis of the distribution of several features within the family Bothriolepididae using the PHYLIP program package provides a new version of the interrelationships of bothriolepids.

KEY WORDS
Vertebrata,
Placodermi,
antiarchs,
Devonian,
Baltic area,
biostratigraphy.

RÉSUMÉ

Bothriolépides antiarches (Vertebrata, Placodermi) du Dévonien du nord-ouest de la plateforme est-européenne.

Une large collection de Bothriolepididae de 26 gisements du nord-ouest de la plateforme est-européenne (Lettonie, Lithuanie, régions de Leningrad, Novgorod et Pskov de la Russie) est étudiée et figurée, avec un traitement critique du matériel précédemment décrit. Le genre *Grossilepis* Stensiö, 1948 est représenté par deux espèces : *Grossilepis tuberculata* (Gross, 1941) et *G. spinosa* (Gross, 1942). Le reste du matériel est attribué au genre *Bothriolepis* Eichwald, 1948 : *B. prima* Gross, 1942, *B. obrutschewi* Gross, 1942, *B. cellulosa* (Pander *in* Keyserling, 1846), *B. panderi* Lahusen, 1880, *B. traudscholdi* Jaekel, 1927, *B. maxima* Gross, 1933, *B. evaldi* Lyarskaja, 1986 du Givétien (?)-Frasnien, et *B. leptocheira curonica* Gross, 1942, *B. ornata* Eichwald, 1840, *B. jani* Lukševičs, 1986, *B. heckeri* n. sp., *B. ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, et une forme non nommée d'âge famennien. La répartition stratigraphique des Bothriolepididae du Dévonien moyen et supérieur du Champ Dévonien Principal et une nouvelle division en zones ichthyologiques sont proposées. Une analyse cladistique des Bothriolepidae utilisant le logiciel PHYLIP a déjà fourni une nouveau scheme de relations de parenté des bothriolépides.

MOTS CLÉS
Vertebrata,
Placodermi,
antiarches,
Dévonien,
Baltique,
biostratigraphie.

CONTENTS

INTRODUCTION

The family Bothriolepididae Cope, 1886 is the most diverse group of antiarchs in the western part of the East European Platform, represented by at least 15 taxa. Subdivision of the Upper Devonian of the Baltic region and north-western part of Russia is based largely on fish data. Bothriolepididae are very important for the correlation of Frasnian and Famennian deposits of the Main Devonian Field of the East-European Platform with similar strata elsewhere. The genus *Bothriolepis* is of particular interest as it is found in the Middle and Late Devonian deposits on all continents.

Gross (1933, 1941, 1942), Lyarskaja (1978, 1981, 1986), Obruchev (1928, 1947, 1958, 1964), Karatajūte-Talimaa (1963, 1966) and others provided lists of agnathans and fishes characteristic for various Devonian beds in the Baltic and north-western part of Russia, described vertebrate assemblages and correlated some strata with the Upper Devonian of other regions. Six new species have been described from the Main Devonian Field since Stensiö's (1948) major revision of the Bothriolepididae. During preparation of this work, a large amount of bothriolepidid remains stored in the main museums of Latvia, Lithuania, Russia and Great Britain was studied. A large amount of new material has been excavated which provided opportunity to revise the structure and distribution of *Bothriolepis* and *Grossilepis* and correlate deposits of various regions. This paper presents the revision of such poorly known species as *Bothriolepis panderi* Lahusen, 1880, *B. traudscholdi* Jaekel, 1927 and *B. ornata* Eichwald, 1840 among 16 taxa of *Bothriolepis* and *Grossilepis* from the Main Devonian Field which have been named and described below, including *Bothriolepis leptocheira curonica* Gross, 1942, moved down to the rank of subspecies.

The placoderm fish material from Latvia and Lithuania comprises numerous well-preserved disarticulated plates, as well as complete head shields and portions of articulated trunk armours. The purpose of this work was to describe and illustrate the armour structure of each species as completely as possible, because the members of the genus *Bothriolepis* are considerably variable in the shape of individual plates and their overlap patterns as well as in the course of sensory line canals.

The largest part of studied and described specimens was collected by J. Blesse, L. Lyarskaja, W. Gross, N. Delle, V. Sorokin, J. Upenieks and the author, and is housed in the Latvian Museum of Natural History (Rīga). Other studied material is in the Paleontological Institute, Moscow (coll. D. Obruchev, R. Hecker, J. Eglons, N. Krupina, F. Chernyshov); Institute of Geology of Lithuania, Vilnius (coll. V. Talimaa); Mining Museum, Saint-Petersburg (coll. H. Helmersen, I. Lahusen, A. Olivieri); Institute of the Earth Crust, St.-Petersburg (coll. A. Ivanov, W. Ermolaew, S. Snigirevsky); Museum of Geology of the University of Latvia, Rīga (coll. N. Delle, R. Kampe); Natural History Museum, London (coll. P. Egerton, J. Eglons, R. Gross); and the National Museum of Scotland, Edinburgh (coll. R. Gross, H. Trautschold, J. V. Rohon).

TECHNIQUE AND TERMINOLOGY

Antiarch remains from the Main Devonian Field are found only rarely as whole skeletons (in four localities only). Well-preserved complete armour of *Bothriolepis evaldi* Lyarskaja, 1986 was found by V. Sorokin for the first time and then several were collected by L. Lyarskaja from an outcrop at the Amula River downstream from Kalnamuiža watermill (Lyarskaja 1986). Prof. D. Obruchev collected whole specimens of *B. traudscholdi* Jaekel at the Syas' River near Stolbovo village. Any skeletal elements behind the trunk armour are not preserved in *Bothriolepis* material from the Main Devonian Field.

Since 1981, the author has collected numerous disarticulated bones of *Bothriolepis* as well as remains of other fossil vertebrates from 26 localities on the Abava, Amula, Ciecere, Daugava, Gauja, Imula, Kaibala, Roja, Skujaine, Svēte,

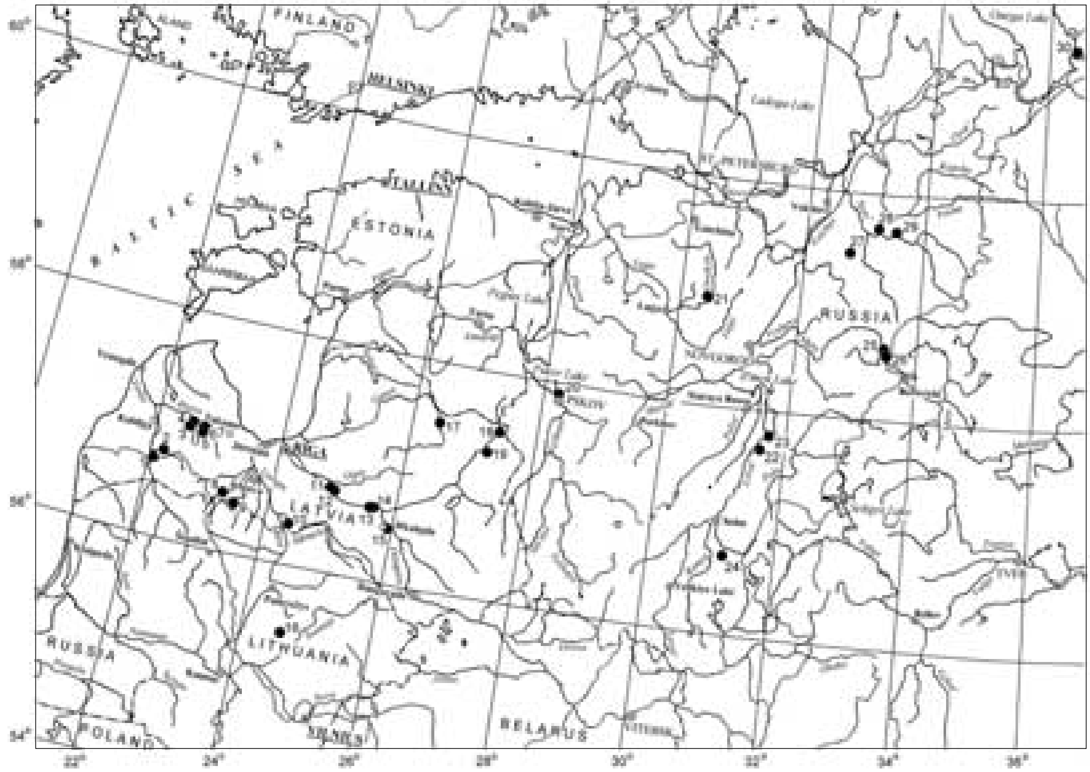

FIG. 1. — Localities of the Main Devonian Field studied by the author and/or mentioned in the text; **1**, Ketleri: *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **2**, Pavāri: *Bothriolepis ciecere*; **3**, Bienes: *Bothriolepis leptocheira curonica* Gross, 1942; **4**, Kalnarāji: *Bothriolepis maxima* Gross, 1933; **5**, Kalnamuiža 1: *Bothriolepis evaldi* Lyarskaja, 1986; **6**, Kalnamuiža 2: *Bothriolepis* sp. (in Amula Formation), *Bothriolepis leptocheira curonica* (in Eleja Formation); **7**, Velna Ala: *Bothriolepis maxima*, *Grossilepis spinosa* (Gross, 1942); **8**, Klūnas: *Bothriolepis ornata* Eichwald, 1840, *B. jani* Luksevics, 1986; **9**, Ķurbes: *Bothriolepis jani*; **10**, Ceraukste: *Bothriolepis maxima*; **11**, Lielvārde: *Bothriolepis maxima, Bothriolepis* sp.; **12**, Kaibala: *Bothriolepis evaldi*; **13**, Koknese: *Bothriolepis cellulosa* (Pander *in* Keyserling, 1846), *Grossilepis tuberculata* (Gross, 1941); **14**, Pastamuiža: *Bothriolepis prima* Gross, 1942 and *B. obrutschewi* Gross, 1942: in Amata Formation; *B. cellulosa*: in Pļaviņas Formation; **15**, Jēkabpils: *Bothriolepis* sp.; **16**, Pelyša: *Bothriolepis prima*, *B. obrutschewi*; **17**, Vidaga: *Bothriolepis traudscholdi* Jaekel, 1927; **18**, Katleši: *Bothriolepis maxima*; **19**, Kuprava: *Bothriolepis* cf. *maxima*; **20**, Piskovichi: *Bothriolepis obrutschewi*; **21**, Yam-Tesovo: *Bothriolepis prima*; **22**, Kurskoye Gorodische: *Bothriolepis maxima* (Obruchev 1947); **23**, Luka: *Bothriolepis maxima* (Obruchev 1947); **24**, Bilovo: *Bothriolepis* sp.; **25**, Lyubitino: *Bothriolepis ornata* (Eichwald 1860); **26**, Zarubino: *Bothriolepis* sp. indet. 1; **27**, Paluitsa: *Bothriolepis maxima* (Ivanov & Khozatsky 1986); **28**, Montsevo: *Bothriolepis panderi* Lahusen, 1880; **29**, Stolbovo: *Bothriolepis traudscholdi*; **30**, Andoma Hill: *Bothriolepis* sp. Dotted line outlines distribution of the Devonian rocks on the subquaternary surface of the Main Devonian Field. The Devonian deposits are not presented to the north of the line, and are covered by the youngest rocks to the south and east.

Šķēde, Venta Rivers, Lode and Jēkabpils quarries in Latvia, Skaistgiris quarry in Lithuania, Syas', Velikaya and Priksha Rivers in Russia (Leningrad, Novgorod and Pskov regions) (Fig. 1). During the field work, the investigations of fossil fish and agnathan localities were made applying the methods suggested by Efremov (1940), taphonomical features were described following the scheme proposed by E. Kurik (Lyarskaja 1981).

Mounted needles and stomatological equipment were normally used. The chemical methods, such as preparation in 7-10% acetic acid solution, were used in some cases.

Outline drawings were mostly prepared from the specimen photos. The photos are usually taken from unprocessed specimens, magnium oxide or ammonium chloride has been used as contrasting agent in some cases. Small object photos were taken using an MFN-5 appliance.

TABLE 1. — Number of measured specimens of bothriolepid taxa, used in statistical analysis. Abbreviations: ***B.***, *Bothriolepis*; ***G.***, *Grossilepis*; **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD1**, dorsal central plate 1; **CV1**, ventral central plate; **La**, lateral plate; **ML2**, lateral marginal plate 2; **MxL**, mixilateral plate; **Nu**, nuchal plate; **PMD**, posterior median dorsal plate; **Pn**, paranuchal plate; **Prm**, premedian plate; **PVL**, posterior ventro-lateral plate.

	Prm	**La**	**Nu**	**Pn**	**AMD**	**PMD**	**ADL**	**MxL**	**AVL**	**PVL**	**CD1**	**CV1**	**ML2**
B. cellulosa (Pander *in* Keyserling, 1846)	9	7	10	7	8	8	–	–	–	–	5	–	–
B. ciecere Lyarskaja *in* Lyarskaja & Savvaitova, 1974	8	13	22	12	21	12	14	30	13	25	18	9	9
B. evaldi Lyarskaja, 1986	8	8	10	9	11	11	7	7	5	5	5	–	7
B. jani Lukševičs, 1986	–	–	6	–	6	5	–	7	–	–	–	–	5
B. leptocheira Traquair, 1893	12	13	15	17	6	–	–	10	7	5	5	5	6
B. maxima Gross, 1933	7	6	10	6	17	9	9	6	6	8	–	5	–
B. obrutschewi Gross, 1942	14	11	8	8	18	24	10	10	–	5	14	7	–
B. ornata Eichwald, 1840	–	6	7	5	10	9	–	5	–	–	–	–	–
B. prima Gross, 1942	–	–	–	–	–	–	–	12	–	13	5	–	6
B. traudscholdi Jaekel, 1927	12	16	21	13	19	24	12	11	14	7	–	8	5
G. tuberculata (Gross, 1941)	–	–	7	6	7	10	–	–	–	–	–	–	–

Measurements were taken with vernier calipers usually on original specimens. For number of statistically analysed measured specimens see Table 1; in cases when the number of measured specimens not exceeds four it is expressed as n in brackets in the text.

Shape and proportions of the whole armour were studied by a method suggested by Karatajūte-Talimaa (1963) using plasticine reconstructions.

Stensiö's (1948) terminology for the bones of Antiarchi is adopted here with some slight alterations suggested by Miles (1968) and Young (1984b) for bothriolepid cheek and jaw plates.

ABBREVIATIONS

GM Mining Museum, Saint-Petersburg;
IEC Institute of the Earth Crust, Saint-Petersburg;
LDM Latvian Museum of Natural History, Rīga;
LGI Institute of Geology of Lithuania, Vilnius;
LUGM Museum of Geology of the University of Latvia, Rīga;
NHM The Natural History Museum, London;
PIN Paleontological Institute of the Russian Academy of Sciences, Moscow;
RSM National Museums of Scotland, Edinburgh;
SMNH Swedish Museum of Natural History, Stockholm;
ADL anterior dorso-lateral plate;
AMD anterior median dorsal plate;
AVL anterior ventro-lateral plate;
ad1, 2 anterior and posterior articular processes on Sm;
alc antero-lateral angle of head-shield;
alr postlevator thickenings of AMD;
a1Sm anterior attachment area for Sm;
a2Sm posterior attachment area for Sm;
a.un unornamented area beneath fossa articularis pectoralis;
CD1-5 dorsal central plates 1 to 5;
CV1-4 ventral central plates 1 to 4;
c.al antero-lateral corner of subcephalic division of ventral lamina of AVL;
cd dorsal crest of AMD;
cf.ADL area overlapping ADL;
cf.AMD area overlapping AMD;
cf.AVL area overlapping AVL;
cf.MV area overlapping MV;
cf.MxL area overlapping MxL;
cf.PVL area overlapping PVL;
cir semicircular pit-line groove;
cit1 crista transversalis interna anterior;
cit2 transverse thickening on the visceral surface of AVL;
cm1 anteromesial corner of ventral lamina of PVL;
cm2 middle corner of ventral lamina of PVL;
cri infra-articular crista of ADL;
crs supra-articular crista of ADL;
cr.o median occipital crista of head-shield;
cr.pl postlevator crista of AMD;
cr.pm paramarginal crista of head-shield;
cr.pto postorbital crista of head-shield;
cr.tp crista transversalis interna posterior;
cr.tv transverse nuchal crista of head-shield;
csl central sensory line groove;

cu postero-ventral ornamented corner of MxL;
d dorsal corner of MxL;
dc dorsal corner of lateral lamina of AVL and PVL;
d.end opening of canal for endolymphatic duct;
dlg1, 2 anterior and posterior oblique dorsal sensory line grooves;
dlm dorsal lamina of ADL;
dlr dorso-lateral ridge of trunk armour;
dma tergal angle of trunk armour;
dmr dorsal median ridge of trunk armour;
dxp dorso-ventral pit-line groove;
f.ap fossa articularis pectoralis;
f.art articular fossa of ADL;
f.ax axillary foramen of AVL;
fe.orb orbital fenestra;
f.mp protractor area of processus brachialis;
fp funnel pit of processus brachialis;
f.retr levator fossa of AMD;
g paired pits on Pp;
grm ventral median groove on dorsal wall of trunk armour;
gr.sc groove, possible for sensory canal;
ifc1 principal section of infraorbital sensory line on head-shield;
ifc2 branch of infraorbital sensory line diverging on La;
La lateral plate;
l lateral corner of PMD;
lc lateral corner of AMD;
lcg main lateral line groove;
llm lateral lamina of ADL;
lpr lateral process of head-shield;
ML2-5 lateral marginal plates 2 to 5;
MM1-3 mesial marginal plates 1 to 3;
MV median ventral plate;
MxL mixilateral plate;
mc lateral corner of Nu;
m.lim margo limitans of AVL;
mp middle pit-line groove;
mppr posterior process on Nu;
mr median ridge of Pp and Prm;
mvr median ventral ridge of dorsal wall of trunk armour;
Nu nuchal plate;
nm obtected nuchal area of head-shield;
npl postlevator notch;
npn postnuchal notch of AMD;
npp postpineal notch of Nu;
nprl prelateral notch of head-shield;
n.prpl notch in dorsal margin of ADL for external postlevator process of AMD;
oa.ADL area overlapped by ADL;
oa.AMD area overlapped by AMD;
oa.AVL area overlapped by AVL;
oa.MxL area overlapped by MxL;
oa.PMD area overlapped by PMD;
oa.PVL area overlapped by PVL;
ood otico-occipital depression of head-shield;
orb orbital margin;
Pi pineal plate;
PDL posterior dorso-lateral plate;
PL posterior lateral plate;
PMD posterior median dorsal plate;
Pmg postmarginal plate;
Pn paranuchal plate;
Pp postpineal plate;
Prl prelateral plate;
Prm premedian plate;
prp posterior process of AMD;
PVL posterior ventro-lateral plate;
p lateral pit of head-shield;
pa posterior corner of PMD;
p.br processus brachialis;
pc postero-lateral corner of Nu;
pe pars pedalis of processus brachialis;
plc postero-lateral corner of PMD;
pma posterior marginal area of PMD;
pnn nasal notch on orbital margin of Prm;
pnoa postnuchal ornamented corner of ADL;
prc prepectoral corner of AVL;
prh preorbital recess of head-shield;
pro processus obstans of trunk armour;
pr.po antero-lateral corner of otico-occipital depression;
pr.pl external postlevator process of AMD;
prv1 anterior ventral process of dorsal wall of trunk armour;
prv2 posterior ventral process of dorsal wall of trunk armour;
pt1 anterior ventral pit of dorsal wall of trunk armour;
pt2 posterior ventral pit of dorsal wall of trunk armour;
Ro rostral plate;
SCLR1, 2 plates 1 and 2 of sclerotic ring;
SM semilunar plate;
Sm submarginal plate;
sgp pectoral pit-line groove;
sna supranuchal area of AMD;
soc anterior section of the supraorbital sensory line on Prm;
socc supraoccipital cross-commissural pit-line groove;
sot supraotic thickening of head-shield;
T terminal plate;
tb ventral tuberosity of dorsal wall of trunk armour;
tlg transverse lateral groove of head-shield;
vlr ventro-lateral ridge of trunk armour.

HISTORICAL ACCOUNT

The generic name *Bothriolepis* was introduced by Eichwald (1840) during the description of materials collected by H. Helmersen and

TABLE 2. — Determination of some specimen from Baltic and Russia, described and referred to *Bothriolepis favosa* by Agassiz 1844-45.

Collector	Plate and figure	Locality	Correct determination
Unknown	pl. 27, fig. 7; pl. 28, fig. 12	Russia	Sarcopterygian lower jaw
Unknown	pl. 28, fig. 13; pl. 30A, fig. 13	Russia	Sarcopterygia
Keyserling	pl. 31A, fig. 32	Saint-Petersburg region	Sarcopterygian operculum(?)
Murchison	pl. 31A, fig. 33	Chudovo, Russia	Bone fragment
Murchison	pl. 31A, fig. 34	Megra, Russia	Bone fragment
Murchison	pl. 31A, fig. 35	Prusino, Russia	Bone fragment

A. Olivieri. Eichwald mentioned *Holoptychius nobilissimus* Agassiz, 1839 and two new taxa, "*Asterolepis*" and *Bothriolepis ornata*, but neither illustrated any samples nor indicated precise localities. Helmersen (1840; see Karatajūte-Talimaa 1963) noted that these fish remains were sampled between Il'men' and Seliger Lakes and at the Msta River, but labels of *Bothriolepis ornata* specimens from the A. Olivieri collection in the Mining Museum (Saint-Petersburg) also give a locality at the Priksha River near Borovichi town in the Novgorod region.

Eichwald (1840) also mentioned *Asterolepis ornata* Eichwald, 1840 and *Bothriolepis prisca* Eichwald, 1840 (original transcription) from the sandstone exposed near Il'men' Lake, and *B. prisca* from the Priksha River, but again without detailed description of these taxa. Later *B. priscus = prisca*? was described from the Middle Devonian deposits at Slavyanka River near Pavlovsk town in the vicinity of Saint-Petersburg (Eichwald 1844b). After studying the specimens, I agree with Obruchev's opinion (*in* Karatajūte-Talimaa 1963) to consider that these remains would belong to Coccosteidae.

In his monograph on the Devonian fishes of the Great Britain and Russia, Agassiz (1844-1845) described *Bothriolepis ornatus* Eichwald, 1840 and *B. favosa* Agassiz, 1844 among others. The remains of *B. ornatus* are shown, as though found by R. Murchison on Priksha River (Agassiz 1844-1845: 149). However, Andrews (1982), using original drawings for the monograph, suggested that these specimens were collected by Robertson in Elgin, Scotland, and belong to *Bothriolepis gigantea* Traquair, 1888, and that *B. ornata* (Andrews 1982: pl. 29, figs 3-5) actually are *B. gigantea* from Monachty Hill near Elgin, Scotland. Other plates (see Table 2) show fragments of "crossopterygian" lower jaws, "crossopterygian" operculum(?), and small indeterminable pieces of bones with more or less pronounced tubercular ornamentation, described by Agassiz as *B. favosa*. This specific name should be therefore treated as a *nomen dubium* and rejected from the list of *Bothriolepis* valid names as it is not based on placoderm fish.

Pander described a new antiarch species from the Upper Devonian marls of Latvia as *Pterichthys cellulosa* Pander *in* Keyserling, 1846 which was referred by Gross (1932) to *Bothriolepis.* Later, Pander (1857) mixed some plates of *Bothriolepis* in the description of *Asterolepis ornata*, and apparently did not recognize the differences between these two genera (e.g., the pectoral fin bone, Pander 1857: pl. 7, fig. 23). Specimens in Pander's collection GM 119, determined by him as *Coccosteus* sp. (GM 1/119, 2/119) and *Asterolepis* sp. (GM 7/119-9/119), have been determined by the author as the remains of *B. panderi* (1/119, 2/119, 7/119, fragments of AVL; 8/119 and 9/119, pieces of pectoral fin bones).

Eichwald (1860) listed the diagnostic features for these genera, several species of *Asterolepis*, and *Bothriolepis ornata* (Eichwald 1860: pl. 56, fig. 3, 1861: pl. 35, fig. 3, Russian edition) and he inaccurately traced AMD from Helmersen's collection (specimen GM 116/107) without mentioning the locality. This bone was later proposed by Woodward (1891) as a type specimen of *B. ornata*.

Lahusen (1880) erected the new species *B. panderi* to commemorate one of the founders of Russian palaeontology. Unfortunately, he did not chose a type specimen. Pl. 1, figs 1, 2 of Lahusen 1880 show the head shield with articulated anterior part of the trunk armour (GM 1/96) found at Syas' River near Montsevo by Pander in 1846. Gross (1932) chose this specimen as lectotype of *B. panderi*. In the pl. 2, figs 2-4, Lahusen (1880) reproduced the head shield, AMD and PMD collected by Trautschold from the other locality at the Syas' River. Trautschold (1880) also provided a detailed description and very superficial reproduction of the same head shield, as well as corrected the shape of Nu and passing of the central sensory line groove in Lahusen's drawings. Later, Jaekel (1927) illustrated this head shield and referred to a new species *Bothriolepis traudscholdi*. Gross (1933: pl. 4, fig. 6) indicated the head shield is kept in Breslau (now Wroclaw in Poland) Museum. Specimens described by Lahusen (1880: pl. 2, figs 2-4) not found neither in Wroclaw, nor in St.-Petersburg (A. Ivanov pers. comm.).

A new period in the study of the Devonian vertebrates and especially antiarchs was started by W. Gross in Latvia and Estonia and D. V. Obruchev in Russia. Obruchev (1928) described sclerotic plates of *B. panderi*, using the lectotype GM 1/96. He improved details of structure of sclerotic plates and provided supplementary arguments in favour of photoreception as primary function of the pineal organ, as well as homologised the pineal plate of *Bothriolepis* with the frontal of osteichthyans.

Gross (1932) published a catalogue of antiarchs, provided a full list of references including works on morphology and ecology, a list of antiarch species and synonyms, as well as a diagram of their geographical and vertical distribution. *Bothriolepis* species from the Main Devonian Field are represented in the catalogue by four taxa: *Bothriolepis ornata*, *B. cellulosa*, *B. panderi* and *B. maxima* Gross, 1933, which were dealt with in more details by Gross (1933). Since Pander had not selected the type specimen of *Pterichthys cellulosa*, Gross chose the head-shield from the type locality (pl. IV, fig. 15; in the text erroneously mentioned fig. 12 reproducing Nu) now kept in the Naturkunde Museum in Berlin. He also noted the presence of smaller bones with tubercular ornamentation rather than with reticular ornament typical for *B. cellulosa* (e.g., Gross 1933: pl. IV, figs 5, 12) from Koknese (Kokenhusen), which were later described as *B. tuberculata* Gross, 1941. Gross (1933) also analysed the structure of the pectoral fin in various groups of antiarchs, and proposed a new terminology for pectoral fin bones which is still in use. He also noted for the first time the presence of two new *Bothriolepis* species in the b-Stufe (Amata Formation sandstone in the modern chart). In his fundamental work on the fishes of the Baltic Devonian and their stratigraphic significance, Gross (1942) described *Bothriolepis prima*, *B. obrutschewi*, *B. spinosa* and *B. curonica*. Due to the political situation in Europe after the Second World War, he was unable to continue this work although a more detailed description of *B. maxima* was supplemented by him in Stensiö's monograph (1948).

Stensiö (1948) reviewed all known species of *Bothriolepis*, and proposed the new genus *Grossilepis* for *Bothriolepis tuberculata* and *B. spinosa*. This classic work provided the most complete description of the morphology of *Bothriolepis*, using the species *B. canadensis*, although some details have since been corrected.

Obruchev (1947) provided short definitions of four species of *Bothriolepis* from Russia and reproduced some bones: PMD of *B. cellulosa* found at Velikaya River near Piskovichi and later placed by him in *Grossilepis tuberculata* (Obruchev 1964: pl. VI, fig. 4); lectotype of *B. panderi*; small head shield of *B. maxima* from Lovat' River; PMD shown by Gross (1933: pl. IV, fig. 14) and Nu of *B. ornata* collected by R. Hecker at Priksha River.

Watson (1961) supplemented details of morphology of *Bothriolepis panderi* based on an exceptionaly preserved specimen from Syas' River provided to him by Obruchev.

Karatajūte-Talimaa (1966) provided detailed descriptions of *Bothriolepis prima* Gross, 1942 and

B. obrutschewi Gross, 1942 including reconstructions of the head-shields and trunk-armours of both species. She also described two new *Bothriolepis* taxa without giving specific names.
Y. Obrucheva (1974) provided a relatively schematic reconstruction of *Bothriolepis maxima* armour based mostly on specimen PIN 1491/41 from Prilovat' Formation, Lovat' River, which consists of a nearly complete head shield, dorsal and ventral walls of the trunk armour and proximal segments of the pectoral fins.
For the Ketleri Formation, Lyarskaja & Savvaitova (1974) established two new species, *Bothriolepis ciecere* and *B. pavariensis* Lyarskaja, 1974, described on a base of few imperfectly preserved bones.
Two new species of *Bothriolepis* from Latvia, *B. evaldi* and *B. jani*, were described by Lyarskaja (1986) and Lukševičs (1986). Lukševičs (1987) provided a more detailed description and reconstruction of *B. curonica* Gross, 1942 trunk armour and (Lukševičs 1992) restudied *B. ornata* type specimen, and collections of Olivieri, Helmersen, Hecker, Talimaa and newly excavated materials and described the type species of the genus *Bothriolepis* in more details.
Denison's (1978) review of all known placoderm fishes listed 46 species of *Bothriolepis*, two species of *Grossilepis* and *Hillsaspis gippslandiensis* (Hills, 1929), the latter referred back to *Bothriolepis* by Young & Gorter (1981). Denison (1978) noted various unnamed *Bothriolepis* forms from many countries, and subsequent descriptions come from Russia (Matukhin *et al.* 1980; Ivanov & Khozatsky 1986; Lukševičs & Sorokin 1999), Kazakhstan (Malinovskaya 1977, 1988, 1992), Iran (Blieck *et al.* 1980), Turkey (Janvier 1983), China (P'an Kiang 1981; Pan Jiang *et al.* 1980, 1987; Pan Jiang 1988), Vietnam (Long *et al.* 1990), North America (Virginia) (Weems *et al.* 1981), Australia (Long 1983; Long & Werdelin 1986; Young 1987, 1990; Johanson 1997; Johanson & Young 1999), Antarctica (Young 1988), South Africa (Long *et al.* 1997), etc. Young published a number of works on biogeography, morphology and phylogeny of placoderms (1974, 1984a, b, 1986). Some papers were dedicated to the morphology of *Bothriolepis* (Werdelin & Long 1986; Young & Zhang 1992), placoderm phylogeny (Janvier & Pan Jiang 1982; Gardiner 1984; Goujet 1984; Goujet & Young 1995) and ecology of ancient animal assemblages including *Bothriolepis* (Novitskaya *et al.* 1983; Lukševičs 1992).

DISTRIBUTION AND BIOSTRATIGRAPHY

Bothriolepidoids are among the most widely distributed and frequently found vertebrates from the Main Devonian Field. The genus *Bothriolepis* is characterised by high diversity and comparatively quick evolution, and is important to biostratigraphy, particularly the correlation of Frasnian and Famennian terrigenous shallow-water deposits of the Main Devonian Field of the East European Platform with strata elsewhere.
One of the earliest reported occurrence of *Bothriolepis* is in the Middle Devonian (Eifelian) of China (P'an 1981), and in the Aztec Siltstone (Givetian) of Antarctica (Young 1988). The oldest remains of *Bothriolepis* in the Main Devonian Field, of probable Givetian age (Gauja Formation), were found in 1964 in borehole material from Latvia (Karatajūte-Talimaa 1966). Unfortunately these remains are lost.
The precise position of the Middle/Upper Devonian boundary on the East European Platform has not been determined as yet (for discussion see Blieck *et al.* in press). This boundary is defined as the base of the lower *P. asymmetricus* conodont Zone, recognized by the first occurrence of *Ancyrodella rotundiloba* Bryant, 1921. Traditionally the base of the Frasnian in the Baltic sequence was placed at the base of the Gauja Regional Stage (Rzhonsnitskaya & Kulikova 1990). Mark-Kurik (1993) regarded the Abava, Gauja and Amata Formations as Givetian, and placed the base of the Frasnian at the base of the Pļaviņas Regional Stage, i.e. at the base of the Pļaviņas Formation and the Snetnaya Gora Beds (see also Ivanov 1993).

TABLE 3. — Distribution of psammosteid, placoderm and acanthodian taxa in the Frasnian of the north-western part of the East European Platform, modified after Ivanov 1990; Ivanov & Khozatski 1986; Lyarskaja & Lukševičs 1992; Esin *et al.* 2000.

Taxa	Regional Stages / Beds*									
	Amata	Pļaviņas			Dubnik	Daugava	Katleši	Pamūšis	Stipinai	Amula
		Snetnaya Gora*	Pskov*	Chudovo*						
Psammolepis undulata (Agassiz, 1844)	—									
Plourdosteus livonicus (Eastman, 1896)	—	—	?	—						
Devononchus concinnus (Gross, 1930)	—									
Psammosteus maeandrinus Agassiz, 1844	—	—	—							
Psammosteus levis Obruchev, 1965	—									
Psammosteus livonicus Obruchev, 1965	—									
Psammosteus praecursor Obruchev, 1947	—	?	—	—						
Psammosteus cuneatus Obruchev, 1965	—									
Psammosteus asper Obruchev, 1965		—								
Karelosteus weberi Obruchev, 1933		—								
Asterolepis radiata Rohon, 1900	—	—	—	—						
Bothriolepis prima Gross, 1942	—									
Bothriolepis obrutschewi Gross, 1942	—									
Plourdosteus mironovi (Obruchev, 1933)		—	—							
Ctenurella pskovensis (Obruchev, 1947)		—								
Grossilepis tuberculata (Gross, 1941)		—	—	—						
Bothriolepis cellulosa (Pander *in* Keyserling, 1846)		—	—							
Bothriolepis panderi Lahusen, 1880		—								
Haplacanthus perseensis Gross, 1942		—	—							
"*Ptyctodus*" sp.		—	—	—	—	—			—	
Rhynchodus sp.		—	—	—						
Rhamphodopsis sp.		—	—							
Psammosteus megalopteryx (Trautschold, 1880)					—	—				
Bothriolepis traudscholdi Jaekel, 1927					—	—				
Asterolepis syasiensis Lyarskaja, 1981					—					
Holonema radiatum Obruchev, 1932					—	—				
Gyroplacosteus panderi Obruchev, 1932					—					
Plourdosteus trautscholdi (Eastman, 1897)					—					
Eastmanosteus egloni (O. Obrucheva, 1956)					—					
Psammosteus falcatus Gross, 1942							—	—		
Psammosteus tenuis Obruchev, 1965							—	—	—	—
Aspidosteus heckeri Obruchev, 1941								—		
Bothriolepis maxima Gross, 1933							—	—		
Devononchus laevis (Gross, 1933)							—	—	—	—
Asterolepis? *amulensis* Lyarskaja, 1981								—		
Bothriolepis evaldi Lyarskaja, 1986								—		
Grossilepis spinosa (Gross, 1942)								—		
Taeniolepis speciosa Gross, 1933								—		

A recent study of conodonts from the stratotypes of the Timan Formation and Ust' Yarega Formation in South Timan by Kuzmin (1995) identified the base of the lower *P. asymmetricus* conodont Zone within the Timan Formation. The upper part of the Timan Formation contains vertebrate assemblages similar to that of the Pļaviņas Formation (Ivanov & Lukševičs 1996). This evidence indicates that lower boundary of the Upper Devonian of the Main Devonian Field should occurs somewhere between the base of

TABLE 4. — Distribution of placoderm, acanthodian and sarcopterygian taxa in the Famennian of the north-western part of the East European Platform, modified after Lyarskaya & Lukševičs 1992; Lukševičs 1995; Esin *et al*. 2000. (Spārnene and Piemare Regional Stages are not officially accepted by the Baltic Stratigraphical Association).

Taxa	Regional Stages / Formations*									
					Spārnene		Piemare			
	Eleja	Joniškis	Kursa	Akmene	Mūri*	Tērvete*	Sniķere*	Žagare*	Ketleri	Škervelis*
Bothriolepis leptocheira Traquair, 1893	—									
Holoptychius cf. *nobilissimus* Agassiz, 1839	—	—	—	—	—	—	—	—	—	—
Phyllolepis sp.			—	—	—	—				
Bothriolepis heckeri n. sp.				—						
Megapomus heckeri Vorobyeva, 1977				—						
Bothriolepis jani Lukševičs, 1986					—	—				
Bothriolepis ornata Eichwald, 1840					—	—				
Homacanthus sveteensis Gross, 1942					—	—	—	—		
Phyllolepis tolli Vasiliauskas, 1963						—				
Chelyophorus sp.						—	—	—		
Dunkleosteus sp.						—		—		
Devononchus tenuispinus (Gross, 1933)						—	—	—	—	
Platycephalichthys skuenicus Vorobyeva, 1962						—	—			
Bothriolepis ciecere Lyarskaja *in* Lyarskaja & Savvaitova, 1974									—	
Devononchus ketleriensis Gross, 1947									—	
Ventalepis ketleriensis Schultze, 1980									—	
Cryptolepis grossi Vorobyeva, 1975									—	
Glyptopomus bystrowi (Gross, 1941)									—	
Orlovichthys cf. *limnatis* Krupina, 1985									—	
Ventastega curonica Ahlberg, Lukševičs & Lebedev, 1994									—	

Pļaviņas Regional Stage, and the base of the Amata Regional Stage.

All studied *Bothriolepis* material from the Main Devonian Field comes from the Upper Devonian deposits (Tables 3; 4). There are 15 bothriolepidid taxa known now from the Main Devonian Field (in chronological order): *Bothriolepis prima, B. obrutschewi, B. cellulosa, B. panderi, B. traudscholdi, B. maxima, B. evaldi, B. leptocheira, B. ornata, B. jani, B. heckeri* n. sp., *Bothriolepis* sp. indet. 1, *B. ciecere, Grossilepis tuberculata, G. spinosa*.

Two broad assemblages characterised by faunal elements associated with the various species of *Bothriolepis* are recognised in the Main Devonian Field (see Esin *et al.* 2000). An older assemblage, identified by the presence of psammosteid heterostracan remains, occurs throughout the Frasnian. There are no psammosteids in the Famennian deposits, which contain the younger broad assemblage (Fig. 2).

LITHOLOGIES, FACIES VARIATIONS AND VERTEBRATE ASSEMBLAGES

Amata Regional Stage corresponds to the Amata Formation in Latvia and Estonia (Fig. 3), upper part of the Šventoji Formation in Lithuania, and Yam-Tesovo Formation in Russia, which are represented mostly by sandstone and clays, usually without invertebrates. The Pļaviņas Regional Stage of Baltic sequence consists of Pļaviņas Formation in Estonia and Latvia, comprising Jara, Suosa and Kupiškis Beds (or Formations: e.g., Narbutas 1994) in Lithuania,

SERIES	STAGE	STANDARD CONODONT ZONATION	MIO-SPORE ZONES	BALTIC REGIONAL STAGES	HETEROSTRACAN ZONES	PLACODERM AND ACANTHODIAN ZONES
UPPER	FAMENNIAN	*praesulcata* *expansa*	SP	Šķervelis Fm		
				Ketleri		*B. cierere*
		postera		Piemare		barren interval
		●		Spārnene		*Phyllolepis* / *B. ornata*
		trachytera				
		● *marginifera*		Akmene		
		● *rhomboidea*	Im	Kursa		
		crepida ●	CZ	Joniškis		barren interval
		triangularis ●	VV	Eleja		*B. leptocheira*
	FRASNIAN	*linguiformis*	DE	Amula		barren interval
		rhenana		Stipinai		
			OG	Pamūšis	*Psammosteus falcatus*	*B. maxima*
				Katleši		
		jamieae		Daugava	*Psammosteus megalopteryx*	*B. trautscholdi*
		hassi	SD			
		punctata		Dubniki		
		transitans		Pļaviņas		barren interval / *B. cellulosa*
		● *falsiovalis*	BI			
MIDDLE	GIVETIAN			Amata		*B. prima* / *B. obrutschewi* — *Devononchus concinnus*
		disparilis	IM	Gauja		*Asterolepis ornata*
		hermanni-cristatus		Abava*		*Watsonosteus*
		varcus	EX	Burtnieki	*P. tuberculatus*	*Diplacanthus gravis*
		hemiansatus		Aruküla	*P. pauli-P. palaeformis*	

and corresponds to the Snetnaya Gora, Pskov and Chudovo Beds in Russia. The deposits corresponding to this stage consist mainly of limestones, marls, dolostones and dolomite marls with abundant and often diverse remains of marine invertebrates. The Snetnaya Gora Beds deposits ("Cellulosa-Mergel" of Gross 1942; the Koknese member of Pļaviņas Formation) are widely distributed all over the Main Devonian Field from Lithuania to Andoma Hill not far from Onega Lake in Russia. These beds contain a rich so called "Snetnaya Gora vertebrate assemblage" (Ivanov 1990), which yields about 20 fish and agnathan taxa (Table 5). This assemblage is represented by three modifications depending on the facial conditions: so-called Jara, Snetnaya Gora *s.s.* and Syas' assemblages. The Jara assemblage occurs in western Latvia and Lithuania, where sandstone, clays and dolostones dominate the sequence, representing sediments originated in a basin with changeable salinity of waters varying from lowered to hypersaline, with large input of terrigenous material.

The Snetnaya Gora *s.s.* assemblage was first described by Gross (1933, 1941, 1942); typical "Cellulosa-Mergel" fauna occurs in central and eastern Latvia, southern Estonia, Pskov region and southern part of Leningrad region. This assemblage partly extends also in the Pskov Beds. Apart form vertebrates the diverse invertebrate fauna evidences gently hypersaline environment with low input of clastic particles. The Syas' assemblage is distributed in north-eastern part of the Main Devonian Field, where terrigenous deposits dominate the sequence (Sorokin 1978). The differences between the modifications of vertebrate assemblages, such as abundance of psammosteid and asterolepid remains, and rarity of dipnoans in sandy parts of the section could be explained by facial changes (Ivanov 1990).

Dubnik Regional Stage of Baltic in the Main Devonian Field is represented by sharply variegated facies and consists of sandstone-clay, limestone-dolomite, clay-carbonate deposits and gypsum, almost everywhere without the remains of animals or plants. It comprises the Salaspils Formation in Latvia, the Pasvalys Beds of the Tatula Formation in Lithuania, and Dubnik Formation in Estonia and Russia. The deposits of this age in Baltic contain scarce remains of undeterminable *Bothriolepis* (Sorokin 1978). In the north-eastern part of the Main Devonian Field, the gypsum and anhydrite are replaced by sandstone, siltstone, clays and marls. Siltstone, silty marls and clays exposured along the Syas' River, contain a rich concentrations of vertebrate remains (at least 14 taxa), lingulids, carbonised plants and ichnofossils (Obruchev & Mark-Kurik 1965; Vorobyeva 1977).

Daugava Regional Stage of Baltic corresponds to the maximum transgression on the territory of the Main Devonian Field and contains mostly carbonate and clayey-carbonate deposits, with thin layers of gypsum and anhydrite in western Latvia (Daugava Formation) and Lithuania (Kirdonys and Nemunelis Beds of the Tatula Formation and the Istras Formation), and with layers of multicoloured sandstone, siltstone and clays in its eastern part (Porkhov, Svinord, Il'men', Buregi, Altovo Beds) (Sorokin *et al.* 1981). The vertebrate remains are very rare and

FIG. 2. — East Baltic Middle-Upper Devonian Regional Stages, vertebrate zones, and their correlation with the conodont dont and spore zones, modified after Blieck *et al.* (in press); Ivanov & Lukševičs 1996; Lukševičs 1995; Kleesment & Mark-Kurik 1997; Valiukevičius 1994. *Abava is Regional Substage being not yet accepted as a Regional Stage by the Baltic Devonian Subcommission. The black dots (•) indicate the conodont zones of the previous Standard Conodont Zonation identified in the succession of the Main Devonian Field (Žeiba & Valiukevičius 1972; Valiukevičius 1994; Kuzmin 1996). Miospore zones after Avkhimovitch *et al.* 1993. Abbreviations: Key to the miospore zones (**Z.**) and subzones (**Subz.**): **BI**, *Acanthotriletes bucerus-Archaeozonotriletes variabilis insignis* Subz.; **CZ**, *Cyrtospora cristifer-Diaphanospora zadonica* Z.; **DE**, *Cristatisporites deliquescens-Verrucosisporites evlanensis* Z.; **EX**, *Geminospora extensa* Z.; **IM**, *Ancyrospora incisa-Geminospora micromanifesta* Subz.; **Im**, *Lagenoisporites immensus* Z.; **OG**, *Archaeoperisaccus ovalis-Verrucosisporites grumosus* Z.; **SD**, *Geminospora semilucensa-Perotrilites donensis* Z.; **SP**, *Spelaeotriletes papulosus* Subz.; **VV**, *Corbulispora vimineus-Geminospora vasjamica* Z. ***B.***, *Bothriolepis*; ***P.***, *Pycnosteus.*

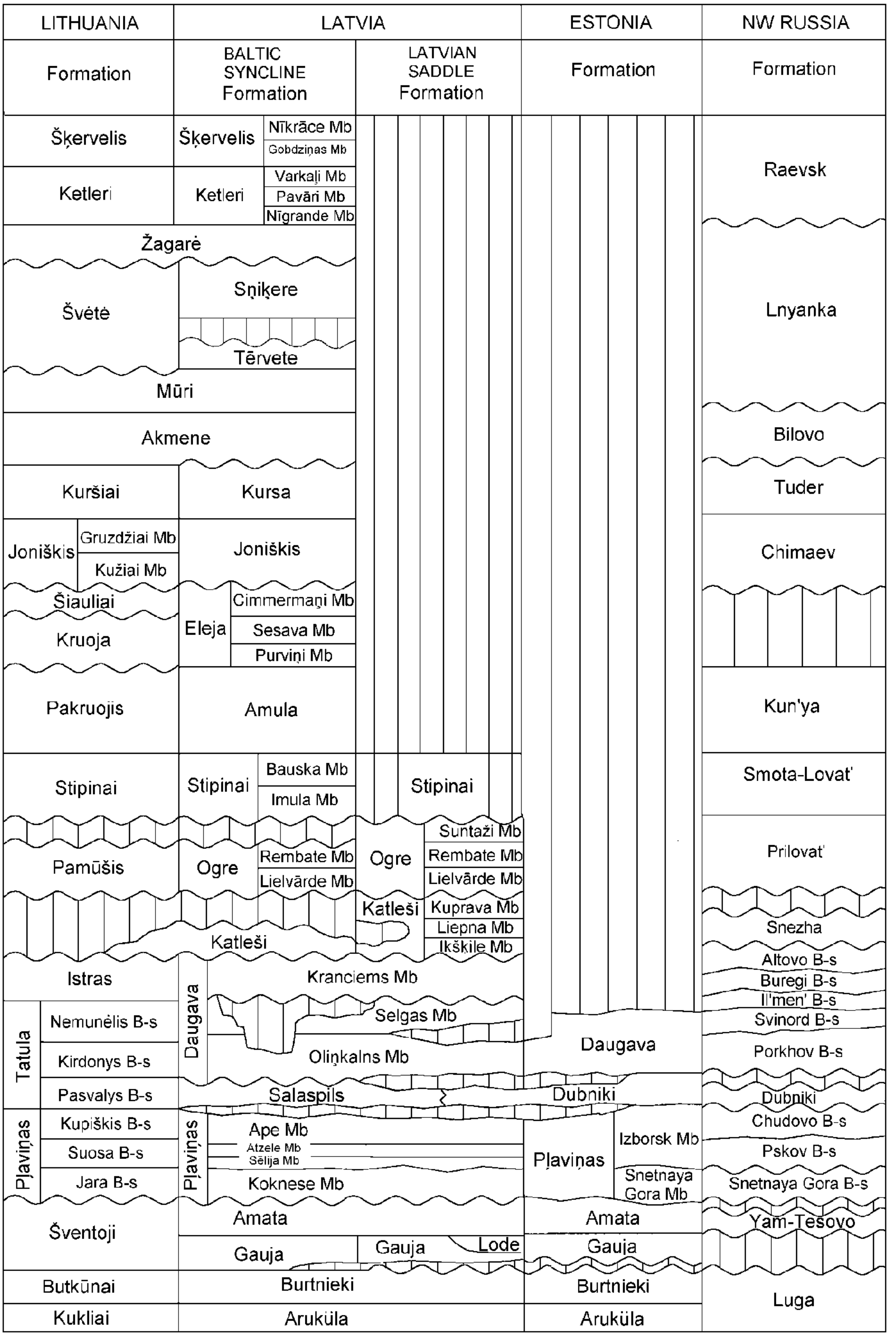

FIG. 3. — Stratigraphic charts of the Middle and Upper Devonian of the East Baltic and NW Russia, after Kleesment & Mark-Kurik 1997; Narbutas 1994; Rzhonsnitskaya & Kulikova 1990; Lukševičs, Mūrnieks & Savvaitova 1999; Gailite *et al.* 2000 (modified). The names of the stratigraphical units of the north-western Russia here and below follows Rzhonsnitskaya & Kulikova 1990. Abbreviations: **B-s**, Beds; **Mb**, Member.

TABLE 5. — Comparison of modifications of the Snetnaya Gora vertebrate assemblages, modified after Sorokin 1978; Ivanov 1990. *, determination by Sorokin 1978. Abbreviations: **A**, abundant; **R**, rare; **V**, very rare.

Taxa	**Jara**	**Snetnaya Gora**	**Syas'**
P. maeandrinus Agassiz, 1844	A	V	A
P. asper Obruchev, 1965			R
Karelosteus weberi Obruchev, 1933			R
Asterolepis radiata Rohon, 1900	A	V	A
Bothriolepis cf. *obrutschewi* * Gross, 1942	R		
Bothriolepis cellulosa (Pander *in* Keyserling, 1846)	A	A	
Bothriolepis panderi Lahusen, 1880			R
Grossilepis tuberculata (Gross, 1941)	R	A	
Ctenurella pskovensis (Obruchev, 1947)		R	V
"Ptyctodus" sp.		V	V
Rhynchodus sp.		V	V
Rhamphodopsis sp.		V	
Plourdosteus mironovi (Obruchev, 1933)		V	A
Strunius rolandi (Gross, 1936)		A	
Latvius grewingki (Gross, 1933)		A	
Eusthenopteron saevesoederberghi Jarvik, 1937	R	R	A
Glyptolepis sp.		R	A
Holoptychius sp.			A
Laccognathus sp.		R	
Rhinodipterus secans (Gross, 1933)	R	A	R
Griphognathus minutidens Gross, 1956		R	
Moythomasia perforata (Gross, 1942)	R	R	R
Chondrichthyes indet.		V	
Acanthodii indet.		V	V

usually poorly preserved in western part of the Main Devonian Field. Fish remains are practically absent in the Buregi Member.

The deposits corresponding to the Katleši Regional Stage in the eastern part of the Main Devonian Field (Snezha Formation in Russia) are represented mainly by variegated facies and consists of carbonate clays and siltstone with thin layers of sandstone and limestone. In Latvia, this regional stage consists of the Katleši Formation. Several levels of the clays and dolomite sandstone of the Katleši Formation contain a quantitatively rich vertebrate assemblages (Sorokin *et al.* 1981). Pamūšis Regional Stage comprises the Pamūšis Formation in Lithuania, Ogre Formation in Latvia and Prilovat' Formation (previous Nadsnezha Beds) in the eastern part of the Main Devonian Field. These formations, consisting mainly of sandstone, clays, marls and dolostones, contain fish remains in the lower part of sequence, usually only in sandstone.

Vertebrates are absent in the Imula and Bauska Beds of the Stipinai Regional Stage (in western part of the Main Devonian Field) and are scarce in the Smota-Lovat' Formation (Russia), which contains no *Bothriolepis*. The Amula Regional Stage, corresponding to the Pakruojis Formation in Lithuania, Amula Formation in Latvia and Kun'ya Beds in Russia, is distributed in Baltic region only in the southern part of western Latvia and north-western Lithuania. It comprises sands and sandstone with layers of siltstone and silty dolostones, which contain the remains of vertebrates in the Lower Amula Member, lingulid shells and ichnofossils, changing with facially variable clays, clayey siltstone, dolomite marls and unfossiliferous dolostones (Sorokin *et al.* 1981).

The Kruoja and Šiauliai Formations in Lithuania and Eleja Formation of Latvia correspond to the Eleja Regional Stage, are suggested to belong to the lower Famennian. Deposits of this interval have no analogues in the eastern part of the

Main Devonian Field. The lower, Purviņi Member of the Eleja Formation is composed mostly of clays with thin layers of sandstone, sometimes of clayey dolostones or dolomite marls, containing vertebrates. The deposits corresponding to the Kursa Regional Stage are distributed in the southern part of western Latvia (Kursa Formation) and north-western Lithuania (Kuršiai Formation) and comprise limestone in their western part, with increasing degree of dolomitization and quantity of clastic material to the east. The limestone yield a rich and diverse invertebrate assemblage consisting of bryozoans, crinoids, brachiopods, worms, bivalves and gastropods (Sorokin *et al.* 1981). Microremains of acanthodians, sarcopterygians, actinopterygians and recently-found elasmobranchs (Ivanov & Lukševičs 1994), as well as macroremains of *Phyllolepis* Agassiz, 1844 were recorded from Kursa Formation dolostones, mostly borehole material. Akmene Regional Stage corresponds to the Akmene Formation, which is distributed over a smaller territory than the Kursa Formation in the southern part of western Latvia and north-western Lithuania. The Akmene Formation everywhere shows two members of dolostones with thin layers of sandstone, siltstone and clays (Sorokin *et al.* 1981). The dolostones contain a diverse assemblage of marine invertebrates, such as brachiopods, bivalves, bryozoans, crinoids and worms, as well as the remains of fishes. Fish remains from the Bilovo Beds, which are usually interpreted as corresponding to the Akmene Formation, are poorly known, but contain the remains of a new species, *Bothriolepis heckeri* n. sp. Spārnene Regional Stage corresponds to the Mūri Formation, occurring in Latvia and Lithuania, the Tērvete Formation of Latvia, and lower part of the Švete Formation of Lithuania (Lukševičs, Mūrnieks & Savvaitova 1999). The sandstone, sand and carbonate sandstone with thin layers of coquinas of the Mūri Formation usually contain well-preserved shells of brachiopods, bivalves, gastropods, nautiloids, crinoid remains and vertebrates. The Tērvete Formation, comprising almost unconsolidated sandstone, dolomite marl and siltstone, in sandy deposits yields the most diverse fish assemblage of the late Famennian age.

Piemare Regional Stage corresponds to the upper part of the Švete Formation in Lithuania, the Sniķere Formation in Latvia, and the Žagare Formation distributed in both countries (Lukševičs, Mūrnieks & Savvaitova 1999). The Sniķere Formation is characterised by more widely represented carbonate deposits, containing brachiopods, bivalves, gastropods, crinoids, ichnofossils and rare vertebrates. The Švete Formation contains sandy dolomites, dolomite marls and siltstone in upper part. Scarce remains of brachiopods, bivalves, conodonts and fishes have been reported from there. The Žagare Formation is represented mostly by dolostones or sandy dolostones with concentrations of brachiopod shells and crinoids, vertebrate remains are rare, usually occurring in sandstone with strong dolomite cement.

Ketleri Regional Stage and the Ketleri Formation, which is subdivided into three members (Lyarskaja & Savvaitova 1974), are distributed in a relatively small territory of south-western part of Latvia and north-western part of Lithuania, comprising sands, sandstone, clays and dolomite marls. The lower, Nigrande Member contains mostly clayey-carbonate deposits, which contain fragments of poorly preserved fishes. The middle and upper, Pavāri and Varkaļi members consist of light-coloured unconsolidated sandstone, more hard sandstone, siltstone, clays and dolomite marls (Lyarskaja & Savvaitova 1974; Lukševičs 1991). Both members are characterised by a diverse fish and primitive tetrapod assemblage (Lukševičs 1991; Ahlberg *et al.* 1994; Lebedev 1995).

The last version of the vertebrate zonation based on the stratigraphic ranges of *Bothriolepis* have been recently proposed for the mostly shallow-water facies, rich in terrigenous deposits, of the Main Devonian Field (Ivanov & Lukševičs 1996; Esin *et al.* 2000). The complete zonation (Fig. 2) consists of four biozones for the Frasnian: *B. prima*-*B. obrutschewi* zone, corresponding to the Amata Regional Stage; *B. cellulosa* zone (Snetnaya Gora and Pskov Beds of the Pļaviņas Regional Stage); *B. traudscholdi* zone (Dubnik and Daugava Regional Stages); *B. maxima* zone (Snezha and Pamūšis Regional Stages); and three zones with one subzone for the Famennian: *B. leptocheira* zone (Eleja Regional Stage); *Phyllolepis* zone (from the Kursa to the Spārnene Regional Stage); *B. ornata* subzone (Spārnene Regional Stage); *B. ciecere* zone (the Pavāri and Varkaļi members of the Ketleri Formation). There are several intervals in the Upper Devonian section possessing scarce vertebrate remains, therefore it is impossible to establish vertebrate zones for such intervals as the Chudovo Beds, the Stipinai, Amula, Joniškis, and Piemare regional stages, as well as the uppermost part of the Baltic Devonian section comprising the Šķervelis Formation.

This vertebrate zonation is useful not only in the Main Devonian Field, but also in adjacent territories, for example in Timan province, where the most part of the Frasnian zones could be traced and correlated with the standard conodont zonation (Ivanov & Lukševičs 1996), and Severnaya Zemlya (Lukševičs 1999a).

SYSTEMATICS

Order EUANTIARCHA Janvier & Pan, 1982
Suborder BOTHRIOLEPIDOIDEI Cope, 1886

Family BOTHRIOLEPIDIDAE Cope, 1886

DIAGNOSIS. — Bothriolepidoids with a small Pp separated from the La by the Nu, which forms part of the posterior margin of the orbital fenestra. AMD with a broad anterior margin; processus obstans strongly developed; PDL and PL replaced by a single MxL; semilunar plate unpaired. Adducted pectoral appendage reaching back beyond trunk shield; central dorsal plate 2 small, and separated from central dorsal plate 1 by lateral and mesial marginal plates 2.

Genus *Bothriolepis* Eichwald, 1840

TYPE SPECIES. — *Bothriolepis ornata* Eichwald, 1840, subsequently designated by Woodward (1891).

DIAGNOSIS. — Bothriolepididae in which the AMD plate is broadest across its lateral corners, and normally overlaps the ADL and is overlapped by the MxL plate. The MxL plate is broadest through its dorsal corner, with its lateral lamina of similar extent to the lateral lamina of the ADL plate, and not forming extensive contact with the AVL plate.

Bothriolepis prima Gross, 1942
(Figs 4-6)

Bothriolepis prima Gross, 1942: 415, 416, abb. 6A.

HOLOTYPE. — AMD, Riksmuseet, Stockholm.

MATERIAL EXAMINED. — Disarticulated plates (LGI 5/1064, 1066, 1072-1074, 1080, 1089, 1215, 2202-2204, 2243, 2245-2247, 2253, 2254, 2264-2270, 2272, 2273, 2286, 2295-2299, 2301, 2302, 2304, 2305, 2307-2311, 2322, 2323, 2325-2327, 2341, 2342, 2383, 2385, 2388, 2398-2406, 2410-2412, 2699-2703). Fragments of the trunk-shield and pectoral fin bones (LDM 43/584) are specimens additional to the material described by Karatajūte-Talimaa (1966) from Pastamuiža locality.

LOCALITIES AND HORIZON. — Daugava River near Pastamuiža in the vicinity of Koknese (Kokenhusen), Latvia; Upper Devonian, lower Frasnian, upper part of the Amata Formation. Pelyša River, Lithuania; uppermost part of the Šventoji Formation. Yam-Tesovo at Oredezh River, Leningrad region of Russia; Staritsa Beds of the Yam-Tesovo Formation.

DIAGNOSIS. — Small *Bothriolepis* with a median dorsal armour length reaching 50 mm. B/L index of the head-shield of 140-150. Weakly convex rostral margin slightly shorter than the posterior margin; obtected nuchal area present only on Nu. Orbital fenestra is relatively large. Nu bears posterior process. Dorsal wall of trunk-armour broad and high in its anterior part and relatively narrow in posterior part, B/L index 77. Lateral wall is high. Tergal angle and median dorsal ridge are weakly defined. Postlevator cristae on the visceral surface of AMD are straight and enclosing a relatively sharp angle. AMD relatively broad, arched, B/L index of 99. Dorsal lamina of ADL relatively narrow, dorsal and lateral laminae enclosing an angle about 122-128°. Angle between the dorsal and lateral walls on MxL is sharper: about 112°. Lateral and ventral walls enclosing an angle about 109° on PVL. Dorso-lateral ridge is weakly defined in its anterior part and is very well-developed in the posterior part of the trunk-shield. Ventro-lateral ridges are strongly developed. Lateral lamina of PVL is 1.7 time as long as it is high. Ventral wall of the trunk-shield is relatively narrow, B/L index of 46, with relatively broad anterior part and narrow posterior part. Lateral and mesial spines on the proximal segment are separate and relatively long. Ornamentation reticulate in small and moderately large individuals, tuberculate in

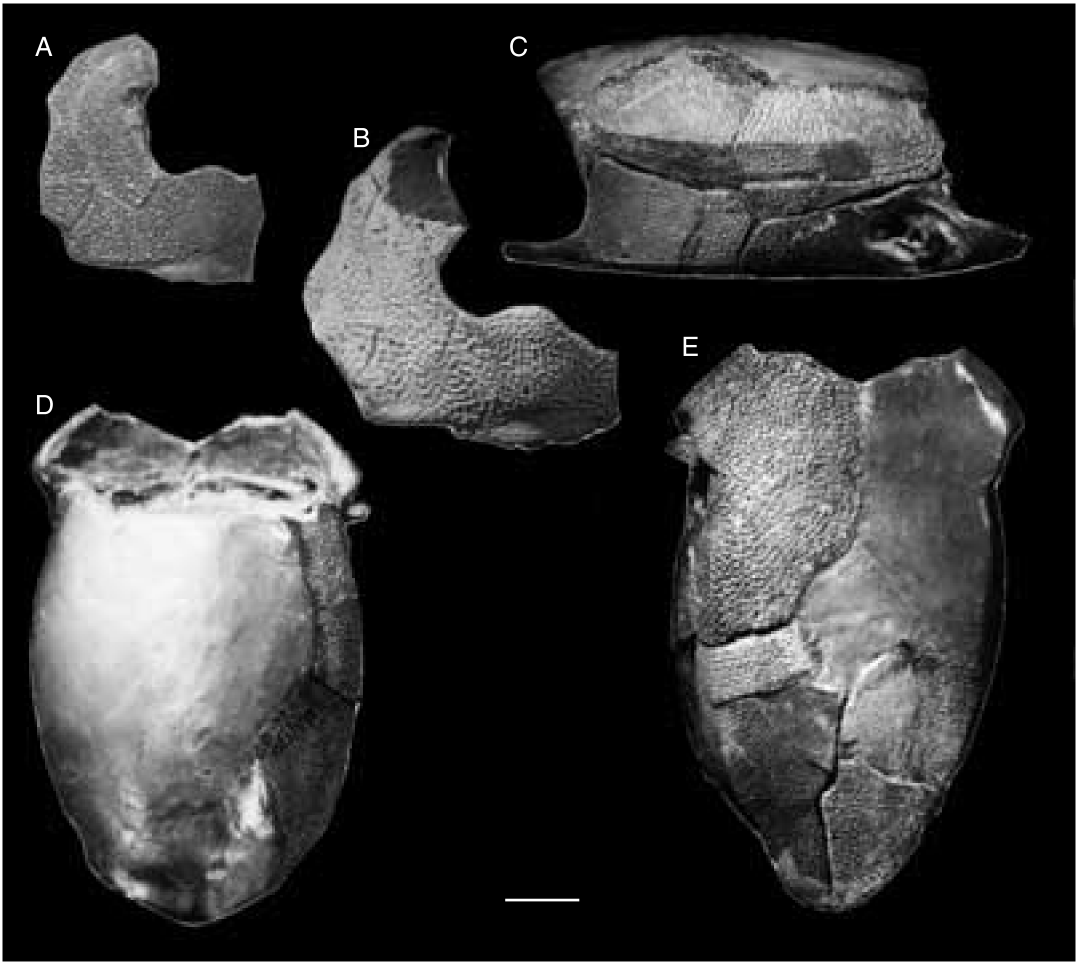

FIG. 4. — *Bothriolepis prima* Gross, 1942; **A**, incomplete head-shield LGI 5-2202; **B**, incomplete head-shield LGI 5-2203; **C**-**E**, restored trunk armour, based on the right ADL LGI 5-2699, MxL LGI 5-2700, AVL LGI 5-2701, right PVL LGI 5-2702 and left PVL LGI 5-2703 in lateral, dorsal and ventral views (produced by V. Talimaa). Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AVL**, anterior ventro-lateral plate; **MxL**, mixilateral plate; **PVL**, posterior ventro-lateral plate. Scale bar: 10 mm.

large individuals. Central part of the dorsal and ventral walls is almost smooth. Pit-line groove crossing the dorso-lateral ridge on the MxL is always present.

DESCRIPTION

As noted by Karatajūte-Talimaa (1966), the head-shield (Figs 4A, B; 5) is strongly vaulted and broad. The antero-lateral corners (alc) and the prelateral notch (nprl) are gently defined. The obtected nuchal area (nm) is relatively broad, well-defined only on the Nu. The orbital fenestra is large, but relatively narrow. Such proportions of orbital fenestra in antiarch fishes is typical for young individuals (Long & Werdelin 1986; Upeniece & Upenieks 1992).

The Prm is moderately broad and short, it is broadest at the antero-lateral corners of the plate. The rostral margin is slightly convex. The orbital margin is concave in specimen LGI 5/1064 from Pelyša River, it is only slightly shorter than the rostral margin (Karatajūte-Talimaa 1966). The infraorbital sensory groove

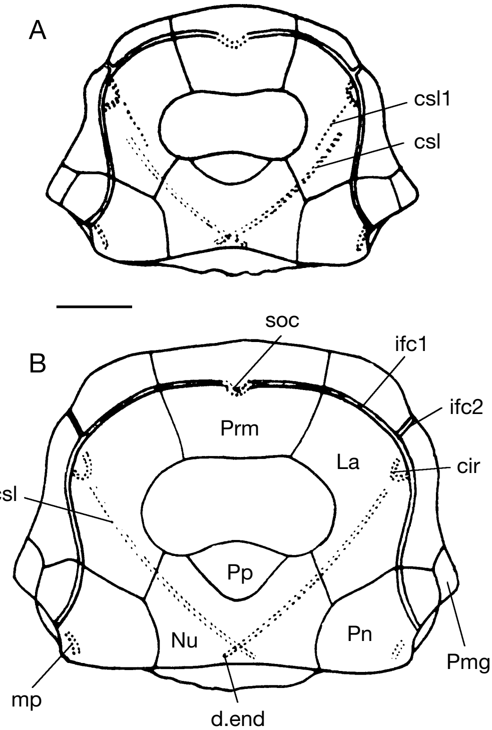

FIG. 5. — The head-shields of *Bothriolepis prima* Gross, 1942, reconstructed by Karatajūte-Talimaa (1966: fig. 1); **A**, based on the head-shield LGI 5-2202; **B**, based on the head-shield LGI 5-2203. Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **cir**, semicircular pit-line groove; **csl**, central sensory line groove; **csl1**, additional branchs of central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **mp**, middle pit-line groove; **soc**, anterior section of the supraorbital sensory line. Scale bar: 10 mm.

crosses the plate in its anterior part, but not so close to the rostral margin as in *B. obrutschewi* (pers. obs.).

The La, Pp and Nu were not described by Karatajūte-Talimaa (1966) in details. The La is moderately broad with the L/B index 140-144, 142 on the average (n = 4). It is narrow in the anterior part and broad in the posterior part. The rostral margin is relatively short and almost straight, the antero-median margin is short. The infraorbital sensory line groove crosses the plate in its anterior part not far from the rostral and lateral margins. The central sensory line groove (csl) finishes at the level of middle of the orbital margin of the orbital fenestra. The Pp is broad in small individuals and of moderate breadth in maturity. Its anterior margin is convex in both small and larger specimens.

The Nu is relatively broad with a L/B index 68-70 (n = 3). The plate is usually broadest across the lateral corners, but in specimen LGI 5/2402 it is broadest across the postero-lateral corners. The anterior division of the lateral margin usually is straight and a little shorter than the strongly concave posterior division. The anterior margin with the deep and broad postpineal notch (Karatajūte-Talimaa 1966). The posterior margin is usually almost straight or slightly concave. The central sensory line groove is clearly distinct. The outer openings of the endolymphatic ducts are small but clearly defined, lying not far from the obtected nuchal area.

The Pn is of moderate breadth, L/B index is 74 and 83 in two measured specimens. The plate bears clearly seen middle pit-line groove (Karatajūte-Talimaa 1966).

The Pmg is broad with the lateral margin slightly longer than the median margin (Karatajūte-Talimaa 1966).

The trunk-armour (Figs 4C-E; 6) is relatively narrow as restored by Karatajūte-Talimaa (1966: figs 3, 4), with broader anterior part of the dorsal and ventral walls of the trunk-armour and much narrower posterior part of that walls, hence broad subcephalic division and narrow and relatively high apperture for the tail. Karatajūte-Talimaa suggested that this fish had narrower and shorter tail than the other representatives of the genus *Bothriolepis*. The length of the dorsal wall reaches about 60 mm. The dorso-lateral and ventro-lateral ridges are well-marked, especially the ventro-lateral ridge and the posterior part of the dorso-lateral ridge. The median dorsal ridge is weakly defined, and is usually better developed posteriorly, on the PMD. The angle enclosed by the dorsal and lateral walls is obtuse in the anterior part of the trunk-armour (measured on the ADL: 122-128°), and is more sharp in the posterior part

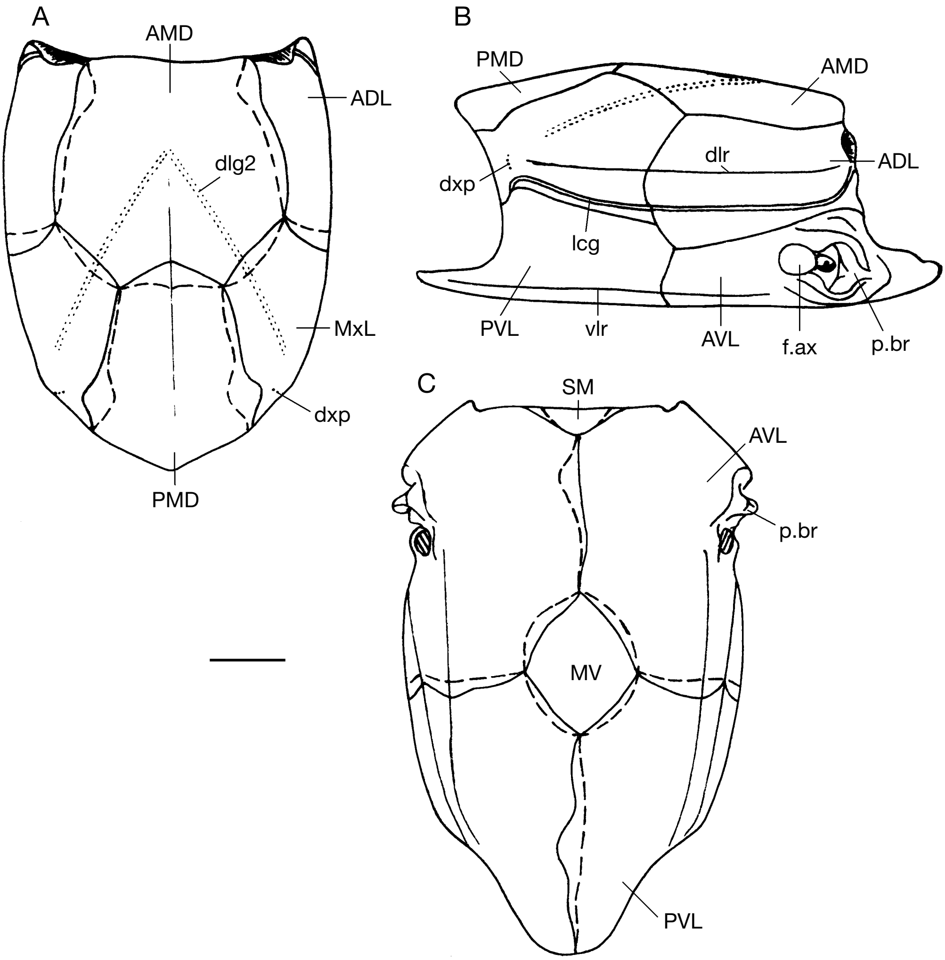

FIG. 6. — Reconstruction of the trunk armour of *Bothriolepis prima* Gross, 1942; **A**, dorsal view; **B**, lateral view; **C**, ventral view (from Karatajūte-Talimaa 1966: fig. 3). Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate; **SM**, semilunar plate; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge of trunk armour; **dxp**, dorso-ventral pit-line groove; **f.ax**, axillary foramen; **lcg**, main lateral line groove; **p.br**, processus brachialis; **vlr**, ventro-lateral ridge of trunk armour. Scale bar: 10 mm.

(on the MxL: 112° on the average). The angle enclosed by the lateral and ventral walls is about 109° (all angle measurements follow Karatajūte-Talimaa 1966).

The AMD is relatively broad, B/L index is 92 and 105 in two measured specimens, characterising by a variable shape. As noted by Karatajūte-Talimaa (1966), the anterior margin is broad, weakly convex, posterior margin short, 1.2-1.8 time shorter than the anterior margin. The antero-lateral and lateral corners are well-defined, but the postlevator processes are weakly developed. The posterior division of the lateral margin is only 1.2-1.9 time shorter than the anterior division (Karatajūte-Talimaa claimed that this feature is rather variable and reaches 1.13-3.22 in *B. prima*, but I did not find the specimens with such an extremely long anterior division of the plate among the material). The median dorsal ridge and the tergal angle (dma) are weakly marked. Overlap areas for the MxL are normally developed as usually in *Bothriolepis*; only in one case for 48 overlooked by Karatajūte-Talimaa (1966), in LGI 5/2247, the AMD overlaps the MxL by its anterior part of the posterior division of the lateral margin similar as in *Remigolepis*. The anterior (dlg1) oblique dorsal sensory line grooves are weakly defined only on the plates of individuals of small size: LGI 5/2247 and 5/1066 with the length of the AMD 13 and 17 mm respectively (pers. obs.). The posterior (dlg2) oblique dorsal sensory line grooves usually are well-defined.

The visceral surface of the AMD shows a slightly lengthened triangular-shaped levator fossa (f.retr), which is limited by the low postlevator thickenings (alr) without the postlevator cristae (Karatajūte-Talimaa 1966), as it is seen in the specimens from Yam-Tesovo, or probably in a posterior part also by the postlevator cristae, as it was figured by Gross (1942: abb. 6A).

The PMD is relatively narrow, B/L index is 75 and 86 in two measured specimens. The posterior margin is usually strongly convex, but rounded, without pronounced posterior corner (Karatajūte-Talimaa 1966). The width of the anterior margin varies between 46-56% of total breadth, being almost of the same proportions as that of *B. obrutschewi*. The lateral corners are well-defined, the postero-lateral corners are often rounded. The median dorsal ridge is usually present only in the posterior half of the plate in well-grown individuals (pers. obs.).

The ADL is moderately broad, the dorsal lamina is 2-2.3 time as long as it is broad and its breadth 1.1-1.2 time exceeds height of the lateral lamina. The dorso-lateral ridge (dlr) is better defined in the posterior part of the ADL (Karatajūte-Talimaa 1966). Dorsal and lateral laminae of the plate enclosing an angle of about 124° on the average (Karatajūte-Talimaa 1966), which is more obtuse than that in *B. obrutschewi*. The processus obstans is strongly developed (Karatajūte-Talimaa 1966).

The MxL was not described by Karatajūte-Talimaa (1966) in details except the proportions, angle between laminae, and sutural connections of the plate. The dorsal lamina of the plate is 1.4-1.7 time as long as it is broad, 1.57 on the average, and possesses a well-defined relatively sharp dorsal corner. The lateral lamina is relatively low, the dorsal length of the plate 2.8-4.1 times (3.6 on the average) exceeds the height of the lateral lamina. The posterior oblique sensory line groove (dlg2) terminates close to the lateral margin, in some distance from the dorso-ventral pitline groove (dxp) crossing the dorso-lateral ridge, similarly to *B. obrutschewi*, but in specimen LGI 5/1072 both grooves are connected with each other. The overlap area for the AMD is usually as normally in *Bothriolepis*, only in one case (LGI 5/2403) it is restricted to approximately one fourth of the length of the antero-dorsal margin (Karatajūte-Talimaa 1966), as in *Remigolepis* (Stensiö, 1931).

The AVL is relatively broad in subcephalic division (Karatajūte-Talimaa 1966), the ventral lamina is 1.5-1.6 time (n = 3) as long as it is broad. The subcephalic division is extremely short and comprises only about 15% of total length of the ventral lamina. The antero-lateral corner is situated slightly medially the axis of the ventro-lateral ridge. The ventral lamina is 2.6-3 times as broad as the low lateral lamina high. The axillary foramen (f.ax) is relatively large and rounded or gently elongated in shape (4.1 × 3.6 mm in LGI 5/2701 with total length of the ventral lamina reaching 33.3 mm).

The PVL is relatively broader than that in *B. obrutschewi*: the ventral lamina is 2.0-2.3 times as long as it is broad. The subanal division occupies about one fourth or fifth (17-26%) of the total PVL length. The lateral lamina is high, the ventral lamina is 1.1-1.5 (1.28 on the average) time as broad as the lateral lamina high. The angle between laminae is more steep as in *B. obrutschewi* and reaches about 109° (Karatajūte-Talimaa 1966). The left PVL overlaps the right one by a wide overlapping area (Karatajūte-Talimaa 1966). The ventro-lateral ridge (vlr) is clearly defined, sometimes slightly pronounced over the lateral lamina.

The MV is typically developed: it is relatively small and of rhombic shape (Karatajūte-Talimaa 1966).

The pectoral fin is represented by several disarticulated bones, and three specimens showing articulated plates of the proximal segment. Karatajūte-Talimaa (1966) claimed that the L/B index of the proximal segment is 3.8-4.5, but I found it to be more elongated being 4-4.6 times as long as it is broad. The CV1 is making contact with the MM2. The distal segment is much shorter than that in *B. obrutschewi*, it is 3.8 times as long as it is broad (Karatajūte-Talimaa 1966). It shows no traces of an individual plates. Probably, Karatajūte-Talimaa (1966) correctly suggested that the pectoral fin does not extend posteriorly far from the posterior margin of the trunk-armour ventral wall. The CD1 is relatively short and broad with L/B index varying from 2.7 to 2.9 (2.8 on the average). The CV1 is slightly longer than the CD1. The ML2 is elongated, proportionally much longer than that in *B. obrutschewi*, it is 4.8-5.1 times as long as it is broad measured from the dorsal side, and 4.1-4.7 times as long as it is broad measured from the ventral side. Both segments bear prominent lateral and mesial spines. The well-defined mesial edge of the proximal segment bears isolated mesial spines and the lateral spines are fused in their base forming well-defined crest (Karatajūte-Talimaa 1966).

The ornamentation was well described by Karatajūte-Talimaa (1966), it is typically reticulate, in small and medium-sized individuals of a fairly regular fine-meshed network of well-defined anastomosing ridges, becoming almost smooth in the middle part of the dorsal wall of the trunk-armour, including the posterior part of the AMD, the anterior part of the PMD, the postero-median part of the ADL, and the antero-median part of the MxL, as well as on the median part of the ventral wall. In rather large individuals ornamentation of the head-shield and dorsal wall of the trunk-armour become more tuberculate. The ornamentation on the subcephalic division of the AVL consists of oblique tubercular ridges, and sometimes there are several tubercular ridges parallel to the posterior margin on the subanal division of the PVL.

REMARKS

The following account is the first full treatment in English, which supplements Karatajūte-Talimaa's (1966) good description (in Russian) of *Bothriolepis prima*, adding some details of structure. It is based mainly on the collections of Karatajūte-Talimaa's and Lyarskaja.

DISCUSSION

Bothriolepis prima resembles *B. obrutschewi* and *B. evaldi* from the Main Devonian field, and *B. hydrophila* (Agassiz, 1844) (Miles 1968) from Scotland. For differences with *B. obrutschewi* and *B. evaldi*, see the descriptions below. *B. prima* differs from *B. hydrophila* in 1) smaller size; 2) broader dorsal wall of the trunk-shield; 3) shape and proportions of the AMD; 4) narrower ventral wall of the trunk-shield; 5) shorter proximal segment of the pectoral fin. *B. prima* can be distinguished from *B. cellulosa* (see Gross 1941), other lower Frasnian *Bothriolepis* representative from the Main Devonian Field mostly by 1) its much smaller size; 2) narrower lateral division of the Pn; 3) proportions of the trunk-armour; 4) narrower PMD; 5) relatively narrower proximal segment of the pectoral fin; 6) CV1, which is making contact with the MM2; 7) smooth median part of the dorsal wall of the trunk armour. Small *Bothriolepis* remains of similar size from Kazakhstan (Malinovskaya 1977, 1988) are too incompletely described and figured to make the detailed comparisons.

***Bothriolepis obrutschewi* Gross, 1942**
(Figs 7-10)

Bothriolepis obrutschewi Gross, 1942: 416-418, abb. 7B.

HOLOTYPE. — MxL Riksmuseet, Stockholm.

MATERIAL EXAMINED. — LGI 5/2248, complete head-shield with articulated anterior part of the trunk armour and proximal segments of the pectoral fin; 5/2249, articulated ventral wall of the trunk armour with proximal segments of the pectoral fin and head-

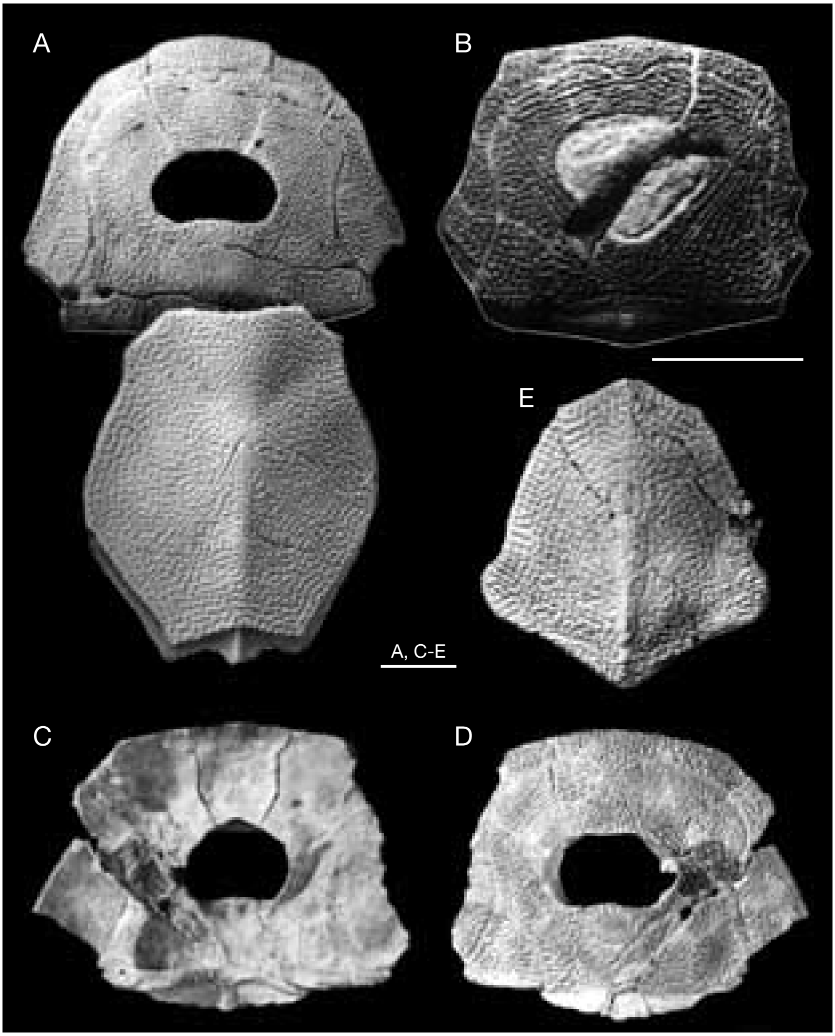

FIG. 7. — *Bothriolepis obrutschewi* Gross, 1942; **A**, head-shield and AMD, probably belonging to the same individual LGI 5-2345; **B**, head-shield of small individual LGI 5-2255; **C**, **D**, head-shield LDM 43/1004, in visceral and dorsal views; **E**, PMD LDM 43/635. Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **AMD**, anterior median dorsal plate; **PMD**, posterior median dorsal plate. Scale bars: 10 mm.

shield in visceral view; 5/2255, 2345, 2598, 2647, articulated head-shields; 5/2213-2235, 2238-2241, 2243, 2247, 2250-2252, 2255-2260, 2262, 2263, 2274-2284, 2288, 2320-2325, 2341-2345, 2350-2354, 2356-2382, 2416-2445, 2447-2450, 2452-2457, 2459-2482, 2484, 2485, 2487-2491, 2498, 2500-2531, 2533-2539, 2552, 2560-2582, 2584-2601, 2603-2615, 2622-2647, 2652-2656, 2659-2661, 2664-2669, 2672, 2674-2683, 2685, 2687-2689, 2697, 2698, LDM 43/1004, articulated head shield; 43/585-671, 43/722: disarticulated plates of the armour from Pastamuiža locality. LGI 5/1099-1101, AMD from Pelyša locality. LGI 5/1216-1222, disarticulated plates of the armour; Paroveja borehole. All this material collected by V. Karatajūte-Talimaa and L. Lyarskaja. LDM 307/1-10, AMD, PMD, ADL, 2 MxL, Nu, 3 CD1 from Pērse locality, samples gathered and presented to LDM by amateur collector Jānis Blesse.

LOCALITIES AND HORIZON. — Pastamuiža locality on the right bank of Daugava River; outcrop on the Pērse River near Koknese close to the type locality, exposure on the left bank of Daugava River near Zvirgzdi,

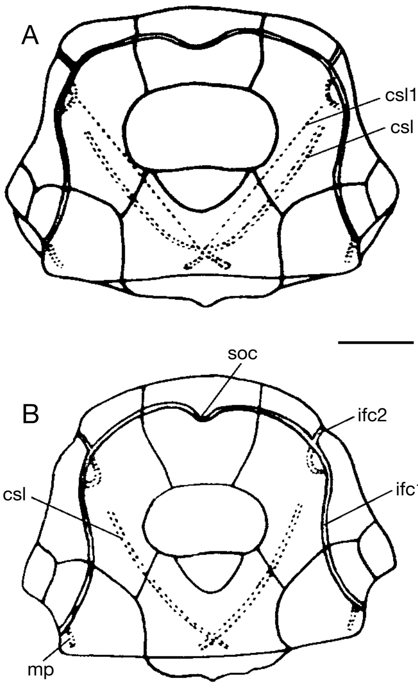

FIG. 8. — The head-shields of *Bothriolepis obrutschewi* Gross, 1942; **A**, head-shield of small individual LGI 5-2255; **B**, head-shield of well-grown individual LGI 5-2345. From Karatajūte-Talimaa 1966: figs 6, 1, 2. Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **csl**, central sensory line groove; **csl1**, additional branchs of central sensory line groove; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **La**, lateral plate; **mp**, middle pit-line groove; **soc**, anterior section of the supraorbital sensory line. Scale bars: A, 5 mm; B, 10 mm.

Latvia; Upper Devonian, lower Frasnian, upper part of the Amata Formation. Pelyša River; Paroveja borehole, 49.65-49.75 m deep, Lithuania; uppermost part of the Šventoji Formation. Piskovichi and Yam-Tesovo, Russia; Podsnetnaya Gora Member of the Yam-Tesovo Formation. Out of the Main Devonian Field this species have been reported (Ivanov & Lukševičs 1996) from the Middle Timan, Uste Chirka Formation and lowermost Uste Srednyaya Beds of the Uste Yarega Formation; and with slight doubt from the North Timan, Kumushka Formation. Probably, the same species occurs in lower part of the Matusevich Formation of Severnaya Zemlya (Lukševičs 1999).

DIAGNOSIS. — *Bothriolepis* of moderate size with a median dorsal armour length reaching 80-85 mm. B/L index of the head-shield 127. Preorbital recess of simple type. Weakly convex rostral margin slightly shorter than the posterior margin. Orbital margin of Prm is straight, without nasal notches. Rostral margin of Prm weakly convex. Anterior and posterior margins of orbital fenestra straight, lateral division of Pn narrow, and Pmg elongated. Dorsal wall of trunk-armour low and relatively narrow (B/L index 86), tergal angle weakly defined, and situated in anterior part of middle third of AMD. Median dorsal ridge on AMD present only in very small individuals, and more clearly defined in PMD. AMD B/L index about 94. Anterior division of the lateral margin is more than twice as long as the posterior division. Overlap area for MxL often of *Remigolepis*-type. PMD B/L index about 91. Dorsal and lateral laminae of ADL enclosing an angle of about 121°. Angle between the dorsal and lateral walls on MxL about 114°. Lateral and ventral walls enclosing an angle about 119° on PVL. Lateral lamina of PVL is relatively high with well-defined dorsal corner. MV is small. Proximal segment of the pectoral appendage of moderate length, 3.8-4.5 times as long as it is broad. Distal segment is relatively long and narrow, 5-5.4 times as long as it is broad. Mesial spines on the proximal segment, as well as dorsal and ventral spines on the distal segment are well-defined, separate and relatively long. Lateral spines on the proximal segment are long and fused in their base forming well-defined ridge. Ornamentation is always reticulate on the ventral wall. Ornamentation of the head-shield and dorsal wall of the trunk-armour, as well as dorsal surface of the proximal segment is tuberculate, which is not always well-defined.

DESCRIPTION

The head-shield in small individuals (Figs 7B; 8A) has a large orbital fenestra and short anterior division (Karatajūte-Talimaa 1966). In larger individuals (Figs 7A, C, D; 8B), the head-shield is moderately broad with B/L index about varying from 123 to 131. In general, the head-shield of *B. obrutschewi* is narrower than that of *B. cellulosa* and *B. prima* (Karatajūte-Talimaa 1966). She shown the rostral margin of the head-shield sometimes bearing the rostral angle, almost straight posterior margin, gently defined antero-lateral corners (alc) and prelateral notch (nprl). Karatajūte-Talimaa (1966) noted that the obtected nuchal area (nm) is relatively broad, well-defined only on the Nu, but I found that in some cases it extends also into Pn. The shape of the preorbital recess was not clearly shown by Karatajūte-Talimaa (1966); it is well seen in a newly prepared specimen LDM 43/1004 being of simple type.

FIG. 9. — *Bothriolepis obrutschewi* Gross, 1942, trunk armour, based on the AMD LGI 5-2632, PMD LGI 5-2561, right ADL LGI 5-2377, left ADL LGI 5-2363, left MxL LGI 5-2498, right AVL LGI 5-2504, left AVL LGI 5-2511, left PVL LGI 5-2252 in lateral, ventral and dorsal views (plasticine reconstruction produced by V. Talimaa). Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate. Scale bar: 10 mm.

The Prm is moderately broad, the B/L index changing from about 134 in smallest individual with the Prm 6 mm long to 94-95 in well-grown individuals with 16-18 mm long Prm. The rostral angle (ac) is present only on the two large Prm. The orbital margin is 1.4-1.8 time shorter than the rostral margin.

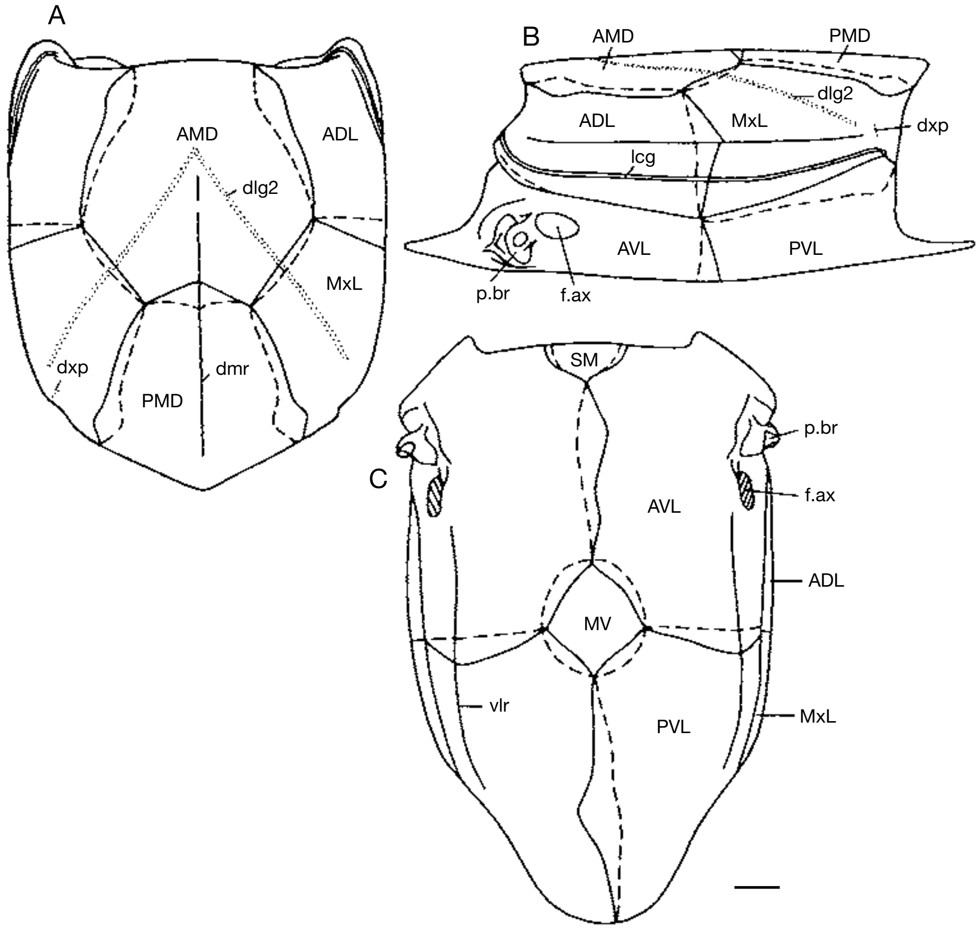

FIG. 10. — The trunk armour of *Bothriolepis obrutschewi* Gross, 1942 reconstructed by Karatajūte-Talimaa (1966: fig. 10); **A**, dorsal view; **B**, lateral view; **C**, ventral view. Daugava River near Pastamuiža, Latvia. Amata Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate; **SM**, semilunar plate; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge of trunk armour; **dmr**, dorsal median ridge of trunk armour; **dxp**, dorso-ventral pit-line groove; **f.ax**, axillary foramen; **lcg**, main lateral line groove; **p.br**, processus brachialis; **vlr**, ventro-lateral ridge of trunk armour. Scale bar: 10 mm.

The La is moderately broad with the L/B index 130-173, 148 on the average. The rostral margin is almost straight, the antero-median and antero-lateral corners are well-defined (Karatajūte-Talimaa 1966). The infraorbital sensory line groove crosses the plate in its anterior part not far from the rostral and lateral margins. The central sensory line groove (csl) usually finishes at the level of the orbital margin of the orbital fenestra. The visceral plate surface shows the antero-lateral corner of otico-occipital depression (pr.po) extending forward slightly over the middle of the orbital fenestra. The transverse lateral groove (tlg) is broad and clearly defined. The lateral pit (p) is broad, shallow and situated equally spaced from an orbital edge of the La and prelateral notch.

The Nu is relatively broad with a L/B index 57-74, 66 on the average. The plate is usually broadest across the lateral corners. The anterior division of the lateral margin usually is straight and a little shorter than the strongly concave posterior division. The posterior margin is usually almost straight, but in LGI 5/2654 it is strongly concave. It always bears the median posterior process (mppr). The central sensory line groove is clearly distinct.

The Pn is of moderate breadth, L/B index about 74-97, 84 on the average. As it was stressed by Karatajūte-Talimaa (1966), the lateral division of the Pn in *B. obrutschewi* is comparatively narrower than that in *B. prima*, *B. panderi* and especially *B. cellulosa* and comprises 42-55% (48% on the average) of the general breadth of a plate. The median division of the plate is broad.

The Pmg is moderately broad with the lateral margin slightly longer than the median margin (Karatajūte-Talimaa 1966).

The Sm (extralateral) plate is known from one specimen, LGI 5/2230 (Karatajūte-Talimaa 1966: pl. IX, fig. 12). It is relatively long with a L/B index of about 250. The dorsal margin has a prominent antero-dorsal process and narrow posterior attachment area for the skull. The posterior margin is strongly convex, the ventral margin is weakly convex. The well-marked lateral notch is rather deep separating the plate into a short thick anterior division and more thin posterior division. There is a groove running along the dorsal margin of the ornamented part of the plate, which is similar to that of *B. macphersoni* Young, 1988. It has the character of a sensory groove.

The trunk-armour (Figs 9; 10) is moderately broad as it was reconstructed by Karatajūte-Talimaa (1966), weakly arched anteriorly and more arched posteriorly with B/L index 86. The length of the dorsal wall, probably, is more than 110 mm. The ventral wall is not quite flat, but slightly arched in rostrocaudal direction. The subcephalic division of the ventral wall is relatively narrow and short. The subanal division of moderate length. The median dorsal ridge is weakly defined, in well-grown individuals it is developed only on the PMD. The dorso-lateral and ventro-lateral ridges are well-marked.

The AMD (Fig. 7A) is moderately broad, B/L index about 89-98, 94 on the average. This plate was well described by Karatajūte-Talimaa (1966). The anterior part of the plate is weakly arched, the posterior part is flattened. The anterior margin may be weakly convex or less often fairly straight. It is relatively narrow. The antero-lateral and lateral corners, as well as the postlevator processes are well-defined. The posterior division of the lateral margin is 1.5-2.3 times shorter than the relatively long anterior division. The median dorsal ridge is weakly defined as a longitudinal row of fused tubercles. Overlap areas for the MxL are normally developed as usually in *Bothriolepis*, but in LGI 5/2215, 5/2639, 5/2697, the AMD overlaps the MxL by its anterior part of the posterior division of the lateral margin similar as in *Remigolepis*. There are some cases the ADL overlaps the AMD in the posterior portion of the common suture: LGI 5/2639, LDM 43/656. The anterior (dlg1) oblique dorsal sensory line grooves are well-defined only on the plates of individuals of small size: LGI 5/2251 and 5/2252 with the length of the AMD 13 and 18.4 mm respectively. The posterior (dlg2) oblique dorsal sensory line grooves usually are well-defined. In some cases the posterior oblique dorsal sensory line grooves are shortened or interrupted (LGI 5/2639), in one specimen (LDM 307/1) there are two parallel branches of this groove on the left side of the plate (pers. observation).

The visceral surface of the AMD shows a slightly lengthened triangular-shaped levator fossa, which is limited by the low postlevator thickenings and in a posterior part also by the postlevator cristae. The anterior ventral pit and the median ventral ridge are well-defined.

The PMD (Fig. 7E) is moderately broad, B/L index about 82-101, 91 on the average. The posterior margin is usually strongly convex, with pronounced posterior corner, but there are specimens with rounded posterior corner noticed. The width of the anterior margin varies between 48-57% of total breadth, it is relatively broader than that of *B. prima*, but narrower than that of *B. cellulosa* (Karatajūte-Talimaa 1966). The lateral corners are well-defined, the postero-lateral corners are often rounded. The median dorsal ridge is present only in the posterior half of the plate in well-grown individuals (Karatajūte-Talimaa 1966). The median ventral ridge and median ventral groove with short posterior ventral pit (pt2) are well-defined on the visceral surface of the plate. The crista transversalis interna posterior (cr.tp) is normally developed, the postmarginal area (pma) is rather broad.

The ADL is relatively broad, the dorsal lamina is 1.9-2.1 times (2.4-2.5 by Karatajūte-Talimaa 1966) as long as it is broad and its breadth 1.2-1.5 time exceeds height of the lateral lamina. The dorso-lateral ridge (dlr) is well-defined. The postnuchal ornamented corner (pnoa) is sharp, moderately long and narrow. Specimen LGI 5/2379 shows the dorsal overlap area partly overlapping the AMD plate. The processus obstans is strongly developed (Karatajūte-Talimaa 1966).

The MxL is moderately broad. The dorsal lamina of the plate is 1.4-1.6 time as long as it is broad. The dorso-lateral ridge is well-defined. The posterior oblique sensory line groove (dlg2) terminates close to the lateral margin, in some distance from the dorso-ventral pit-line groove (dxp) crossing the dorso-lateral ridge. Specimen LDM 307/6 has no posterior oblique sensory line groove. The overlap area for the AMD is often restricted to half the length of the antero-dorsal margin (Karatajūte-Talimaa 1966) (LGI 5/2485, 5/2490, 5/2491), as in *Remigolepis* (Stensiö 1931).

The ventral lamina of the AVL is 1.6-1.8 time as long as it is broad. The subcephalic division is short and comprises about 20% of total length of the ventral lamina. The antero-lateral corner is situated slightly medially the axis of the ventro-lateral ridge. The ventral lamina is 2.9-3 times as broad as the low lateral lamina high. The right AVL overlaps the left AVL. The axillary foramen (f.ax) is relatively large and rounded or slightly elongated in shape (Karatajūte-Talimaa 1966). The visceral surface of the AVL shows the high transverse anterior crista running almost mesially subparallel to the gently defined low and broad transverse thickening (Karatajūte-Talimaa 1966), but nevertheless a sharp angle between cit1 and cit2, unlike as in *B. ciecere* or *B. karawaka* Young, 1988 is clearly seen.

The PVL has similar proportions to the AVL, as in most *Bothriolepis* species. It is of moderate breadth, the ventral lamina is 2.1-2.6 times as long as it is broad. The subanal division is relatively broad (Karatajūte-Talimaa 1966), it occupies about one forth (23-28%) of the total PVL plate length. The lateral lamina is moderately high, it is relatively higher than that in *B. prima* (Karatajūte-Talimaa 1966); the ventral lamina is 1.2-1.3 time as broad as the lateral lamina high. The ventro-lateral ridge (vlr) is well-defined.

The pectoral fin is represented by many disarticulated bones, and five specimens showing articulated plates of the proximal segment. There are 14 examples of the distal segment or it fragments. The CV1 contacts the MM2. The CD1 is of moderate size with L/B index varying from 2.7 to 3.1 (2.8 on the average). The CV1 is slightly longer than the CD1 and have the L/B index about 3.1-3.4 (3.2 on the average). The ML2 is 4.2-4.4 times as long as it is broad. The distal segment shows only CD3. Both segments bear prominent lateral and mesial spines. On the proximal segment the isolated mesial spines are large and high.

The ornamentation is generally tubercular with coarse tubercles and short vermiculated ridges of fused tubercles on the head-shield in well-grown individuals (Karatajūte-Talimaa 1966). The short radially arranged ridges are developed along the margins of the La and Nu. The network of anastomosing ridges, which are broken into short ridges could be sometimes seen on the posterior part of the Prm. The ornament on the Sm consists of the network with weak elevations in the points of anastomoses on the central part of the plate and is almost smooth on the posterior part. The ornament is typically tubercular in general on the dorsal and lateral walls of the trunk-armour and reticular on the ventral wall (Karatajūte-Talimaa 1966). The tubercles are usually relatively low, often fused forming the short, sometimes vermiculated ridges. The tubercles and ridges are arranged into rows, parallel to the mesial margin of the ADL and anterior margin of the MxL. The ornamentation is fine-tuberculated on the lateral wall of the trunk-armour. The ornamentation of the pectoral appendage also is variable. It is reticulate in general, on the CD1 the ornament consists of radially arranged ridges of fused or isolated tubercles. The network of ridges bears weak elevations in the points of anastomoses on the ML2 and CV1. The distal segment bears the longitudinal well-defined ridges on the dorsal wall. The ventral wall of the distal segment is almost smooth with gently defined ridges in its proximal part.

REMARKS

The above account is the first full treatment in English, which supplements Karatajūte-Talimaa's description (in Russian) of *Bothriolepis obrutschewi* (1966), using specimens from the collection of the Latvian Museum of Natural History and adding some details such as structure of the visceral surface of the head shield.

DISCUSSION

Bothriolepis obrutschewi resembles *B. prima*, but may be distinguished by 1) its narrower head-shield; 2) relatively broader dorsal and ventral walls of the trunk-armour; 3) relatively longer subanal division of the PVL; 4) shape of the postlevator cristae on the visceral surface of the AMD; 5) proportions of the ADL; 6) more strongly defined tubercular ornament; 7) development of the central sensory line groove (csl) and the anterior oblique dorsal sensory line groove (dlg1) in smallest individuals. *B. obrutschewi* differs from *B. evaldi* in its 1) much broader dorsal wall of the trunk-shield; 2) shape and proportions of the AMD; 3) shape of the post-nuchal ornamented corner of the ADL; 4) narrower ventral wall of the trunk-shield; 5) shorter proximal segment of the pectoral fin.

B. obrutschewi resembles *B. panderi* by the ornamentation, but differs from it in 1) shape and proportions of the head shield; 2) proportions of the lateral division of the Pn, which is narrower in *B. obrutschewi*; 3) broader AMD; 4) relatively narrower anterior margin of the AMD; 5) relatively shorter pectoral fin.

B. obrutschewi can be distinguished from *B. cellulosa* (Gross 1941), other lower Frasnian *Bothriolepis* representative from the Main Devonian Field in 1) its smaller size; 2) tubercular ornamentation; 3) narrower head-shield; 4) shape of the Prm possessing more long orbiral margin; 5) course of the infraorbital sensory line groove on the Prm and La; 6) shape of the Nu; 7) narrower lateral division of the Pn; 8) longer Sm; 9) features of the visceral surface of the trunk armour; 10) CV1, which is making contact with the MM2.

Bothriolepis cellulosa (Pander *in* Keyserling, 1846) (Fig. 11)

Pterichthys cellulosa Pander *in* Keyserling, 1846: 292.

Bothriolepis retinata Hoffman, 1911: 293, 297, figs 14, 15; pl. 24, fig. 4. — Gross 1931: 58. — Stensiö 1931: 11.

Bothriolepis cellulosa (Pander) – Gross 1932: 24; 1933: 36-39, figs 36-39; pl. 4, figs 1, 9, 10, 12, 15; pl. 5, fig. 12 (in part).

TYPE SPECIMEN. — The head-shield f 147, Museum für Naturkunde, Berlin, chosen by Gross among specimen collected from the type locality (Gross 1933: taf. 4, fig. 15).

MATERIAL EXAMINED. — (Addition to the descriptions of Gross [1941] and Stensiö [1948]). LDM 43/673: fragment of the AMD; LUGM 6, 9, 10: AMD; LUGM 2, 9, 12, 14: PMD; LUGM 5, 16: MxL; LUGM 2, 9, 13, 17: bones of the pectoral fin; LUGM 2, 4, 8, 15: head-shields; NHM P.17807, 17810, 17813, 17814, 17818, 17826, 17828, 17829, 17836, 17837: Nu, AMD, 2 PMD, 4 MxL, AVL, four fin bones; RSM 1964.26.41 (SMNH P.3275): impression of the AMD and AVL.

LOCALITIES AND HORIZON. — The type locality is an outcrop of dolomites, dolomite marls and clays at the right bank of Pērse River (right tributary of Daugava River) near Koknese (Kokenhusen). The other studied material comes from Pastamuiža on Daugava River, Latvia; the lower Frasnian Pļaviņas Regional Stage: Snetnaya Gora, Sēlija and Ātzele Members of the Pļaviņas Formation; and outcrop at the right bank of Velikaya River in Pskov near Piskovichi, Russia; Snetnaya Gora and Pskov Beds. The remains of this species were found in the

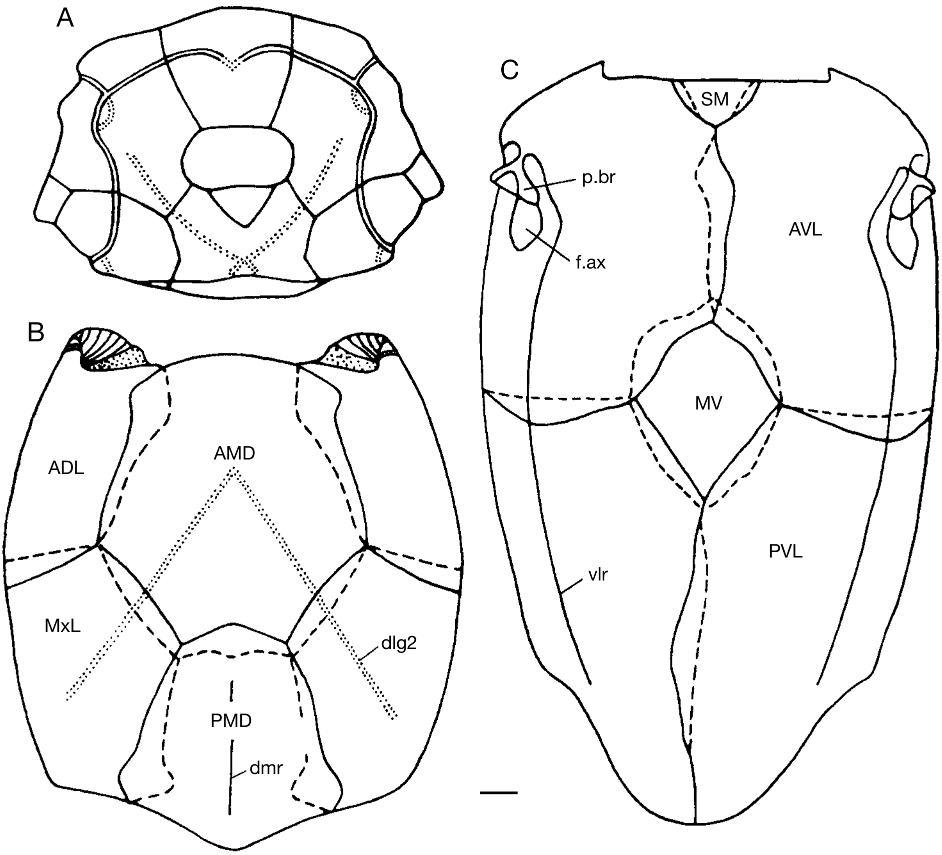

FIG. 11. — **A**, head-shield of *Bothriolepis cellulosa* (Pander *in* Keyserling, 1846), lectotype (from Gross 1941: abb. 7 D); **B**, **C**, reconstruction of the trunk armour of *Bothriolepis cellulosa* in dorsal and ventral views (from Gross 1941: abb. 17, 18). Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate; **SM**, semilunar plate; **dlg2**, posterior oblique dorsal sensory line groove; **dmr**, dorsal median ridge of trunk armour; **f.ax**, axillary foramen; **p.br**, processus brachialis; **vlr**, ventro-lateral ridge of trunk armour. Scale bar: 10 mm.

Snetnaya Gora Member in several localities in western and eastern Latvia, e.g., outcrops along Daugava River from Kaktiņi to the ruins of Koknese castle, exposures at Amata River near Kārļi and along Mazā Jugla and Lielā Jugla rivers, outcrops at Venta River near Kuldīga and at Riežupe River near Kaļķi hamlet; Lithuania: borehole Berčiunai, 73-76 m deep, borehole Pakapiai, 78.2-80.3 m deep. Additionally, *B. cellulosa* was correctly reported from more easterly boreholes at the middle reaches of Onega River in Arkhangelsk region of Russia (Ivanov 1990), in Izborsk (Slavyanskie Klyuchi), at Ostenka River, in the Yam-Tesovo locality (pers. comm., A. Ivanov), borehole 7-Ost.-Staraya Russa, 154.4-152.0 m deep (Sorokin 1978: determination of D. Obruchev), as well as from Ukhta River, South Timan, Lower Ust' Yarega Formation, and from Pizhma River of the Middle Timan, the Ust' Srednyaya Beds and the Srednyaya Beds of the Ust' Yarega Formation (Ivanov & Lukševičs 1996).

DIAGNOSIS. — *Bothriolepis* of moderate size with a median dorsal armour length of at least 190 mm. Head-shield is relatively broad, B/L index of 128-146, 138 on the average, and comparatively flat in its preorbital division. Anterior margin of the head-shield is considerably shorter than posterior margin, slightly convex and rounded with a rostral angle. Preorbital recess of simple type. Prm is broad, posterior margin is much shorter than the anterior margin. Pineal plate broader than long or about as broad as long. Nu is broad, L/B index of 65-81, 70 on the average. Lateral division of Pn is comparatively broad. Dorsal wall of the trunk armour is not high and of moderate width. Tergal angle is situated in the foremost part of the middle third of the AMD. Median dorsal ridge is weakly developed and partly absent in large individuals. Postlevator crest usually present and often very strongly developed in its posterior part, forming there to a certain extent a floor beneath the levator fossa. Ventral tuberosity practically absent. AMD is moderately broad, B/L index 83-94, 89 on the average. PMD comparatively broad with B/L index 82-112, 96 on the average; anterior margin is broad, posterior corner obtuse or rounded off. Pectoral fin fairly robust. Proximal segment is moderately long, 3.5 to 4 times as long as broad. The point contact between MM1 and CV2 plates of pectoral fin results in separation of CV1 from MM2. Lateral spines of proximal segment comparatively short. Medial spines fairly strongly developed and independent; the median spines situated on the CD1 and on the adjacent parts of the MM2 pointing dorsally. Ornamentation typically reticulate, in small and medium-sized individuals of a fairly regular fine-meshed network of anastomosing ridges, narrow and well-defined and with distinct tubercular thickenings and elevations at their points of union. Ornament in quite lagre individuals retaining an on the whole fine-meshed reticular character on the head-shield, but often dissolved into tubercles and nodose tubercular ridges on the dorsal wall of the trunk armour.

Remarks

Bothriolepis cellulosa is well-described by Gross (1941) and Stensiö (1948) and its diagnosis is to the large extent based on their descriptions, except for the measurements and estimated indices.

Discussion

Bothriolepis cellulosa resembles *B. panderi* in certain aspects, but differs from it in 1) the shape and proportions of the Prm; 2) the shape of the Pi; 3) the shape and forward extension of the Pn in *B. panderi*; 4) the robust and relatively shorter proximal segment of the pectoral fin; 5) character of ornamentation. (For the comparison of *B. cellulosa* with *B. prima* and *B. obrutschewi*, see the descriptions of the latter presented above).

B. cellulosa is most closely resembling *B. canadensis* (Whiteaves, 1880) in several respects and differs from this species just slightly in its 1) narrower and more flattened head-shield; 2) narrower orbital fenestra; 3) broader lateral division of the Pn; 4) shorter and higher submarginal plate; 5) structure of the visceral surface of the AMD; 6) character of the ornamentation in large individuals. These two species seems to be phylogenetically very closely related.

Bothriolepis panderi Lahusen, 1880 (Figs 12; 21J)

Bothriolepis panderi Lahusen, 1880: 137, taf. 1, figs 1-5; taf. 2, fig. 1 [non Figs 2-4]. — Gross 1932: 25 (in part).

Lectotype. — The complete head shield and anterior part of the trunk armour MM 1/96, chosen by Gross (1932).

Material examined. — SMNH P.3387, CD1; MM 2/96, 3/96, fragments of the pectoral fin; LDM 63/337, AVL, 63/338, ADL; GM 1/119, 2/119, 7/119, fragments of AVL, 8/119 and 9/119, pieces of pectoral fin bones. These bones and lectotype is all so far available material.

Locality and horizon. — Right bank of Syas' River not far from Montsevo village, Russia; the lower Frasnian Snetnaya Gora Beds.

Diagnosis. — *Bothriolepis* with a median dorsal trunk armour length of at least 125 mm. B/L index of the head shield is 147. Rostral margin is convex, much shorter than the posterior margin. Orbital fenestra is relatively small, short and broad, with a B/L index 180. Prm is relatively broad, B/L index is 100; the slightly convex orbital margin is much shorter than the rostral margin. Rostral plate is twice as broad as it is long and bears deep and short nasal notch. Pineal plate is relatively broad with the concave anterior and lateral margins; the posterior margin is almost stright. Outer surface of the plate is pierced by the pineal opening. Nu relatively broad, L/B index of 61. Pmg is longer than broad with lateral margin much longer than the median margin. Trunk-armour is relatively broad, with somewhat elevated dorsal wall. AMD is moderately broad, B/L index about 71. The anterior margin is moderately broad, 1.5 time shorter than the maximum breadth of the plate. The postlevator processes are strongly defined. Median dorsal ridge poorly developed. AVL is of moderate breadth with short subcephalic division; the anterior lateral corner of subcephalic division is situated in the middle between the median and lateral margins. Proximal segment of the pectoral appendage is relatively long and slender, about five times as long as it is broad; it bears prominent lateral and mesial spines, the mesial ones are numerous, short and closely setting. CD1 of moderate size, L/B index about 2.6. The ornamentation consists of tubercles and short vermiculated ridges both on the head-shield and the trunk-armour.

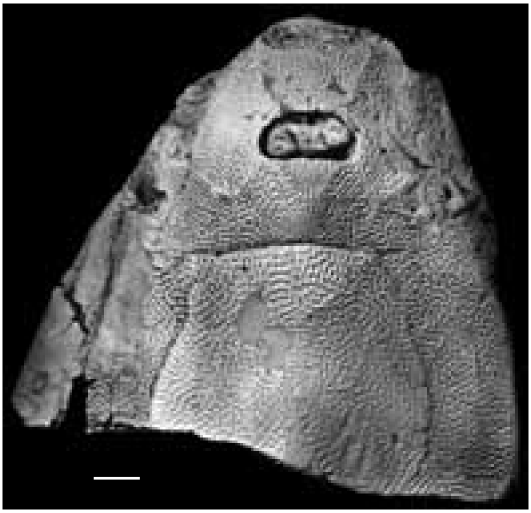

FIG. 12. — *Bothriolepis panderi* Lahusen, 1880, lectotype, the complete head-shield and anterior part of the trunk armour MM 1/96. Right bank of Syas' River near Montsevo village, Russia. Snetnaya Gora Beds. Scale bar: 10 mm.

DESCRIPTION

Bothriolepis panderi attained a somewhat larger size than *B. cellulosa*. The length of the head shield reaches about 60 mm, the dorsal length of the trunk armour is estimated at least about 125 mm. The proportions and shape of the head-shield resemble that of *B. canadensis*, but differs well from that in *B. cellulosa*. It is comparatively flat in its anterior part and slightly vaulted in the posterior part. It seems to be relatively shorter than that in *B. cellulosa*.

In almost all aspects, the Prm looks similar to that in *B. cellulosa* and *B. canadensis*. It is broadest at the infraorbital sensory groove or rostral margin. The orbital margin seems to be devoid the nasal notch. The rostral margin is not well-preserved in the lectotype and hence it is impossible to decide whether or not the rostral angle is presented.

The La on the both sides of the lectotype are crushed and therefore do not show several characters. The rostral margin seems to be of moderate breadth. The infraorbital sensory groove crosses the plate not far from its lateral and rostral margins. The central sensory line groove is finished slightly anteriorly the level of middle of the orbital fenestra length.

The Ro is much broader and shorter than in *B. canadensis*. The Pi is relatively broad, breadth slightly exceeds a length. The Pp is short and broad, L/B index is 156, with a slightly convex anterior margin.

The Nu is deficient posteriorly, but seems to be relatively broad with a L/B index of about 61. The anterior division of the lateral margin is concave and a little shorter than the posterior division. There are short supraoccipital grooves, which terminate little in front of the obtected nuchal area at the rather large external openings for the endolymphatic ducts.

The Pn is of moderate breadth, L/B index 82. The lateral division of the Pn is relatively narrow and is composing 49% of the general breadth of a plate.

Three sclerotic plates in most features are similar to that of *B. canadensis* (Stensiö 1948: text-fig. 21).

The dorsal wall of the trunk armour is higher than that in *B. cellulosa*. The median dorsal ridge is rather weakly developed, and both dorso-lateral and ventro-lateral ridges are well-marked. The anterior margin of the AMD is weakly convex. The antero-lateral and lateral corners are rounded. The posterior division of the lateral margin seems to be much shorter than the anterior division. The tergal angle (dma) is situated in between the anterior and middle thirds of the plate and is weakly marked. Overlap areas for ADL and MxL are normally developed as usually in *Bothriolepis*.

The dorsal lamina of the ADL is relatively narrow and long, with massive postnuchal ornamented corner. A new specimen of AVL collected from the type locality shows the anterior lateral corner of subcephalic division, which is situated in the middle between the median and lateral margins and developed into a short broad process (c.al, Fig. 21J). The visceral surface of this specimen demonstrates the high transverse anterior crista (cit1) running antero-mesially and low and broad transverse thickening running more mesially.

REMARKS
Lahusen (1880) erected a new species *B. panderi* for the remains of bothriolepids collected by Pander & Trautschold from several localities at the Syas' River. For the head-shield coming from Stolbovo locality and illustrated by Lahusen (1880: taf. 2, figs 2-4), Jaekel (1927) erected a new species *B. traudscholdi*. Gross (1932) proposed the head-shield MM 1/96 as a lectotype of *B. panderi* and mentioned *B. traudscholdi* as synonimous to *B. panderi* without any comments. Stensiö (1948) provided an extensive description of this species, based on the material described by Lahusen (1880), Trautschold (1880) and Gross (1933). In 1988, the author collected fragmentary AVL and ADL form the type locality, and revisited all available material from Syas' River. In my opinion, specimens from the Stolbovo site belongs to separate species, namely *B. traudscholdi* (see below). Therefore the description of *B. panderi* provided here differs greatly from those given by Gross (1933) and Stensiö (1948).

DISCUSSION
Bothriolepis panderi closely resembles *B. cellulosa*, but differs from it in features mentioned above in the description of *B. cellulosa*. This species also seems to be closely related to *B. canadensis*, but differs in 1) position of the infraorbital sensory groove; 2) much broader rostral plate; 3) higher dorsal wall of the trunk-armour; 4) more slender proximal segment of the pectoral fin.

The species *B. panderi* and *B. taylori* Miles, 1968 from Edenkillie Beds of Scotland (Miles 1968) are clearly very close morphologically. They are similar in 1) the general proportions of the trunk-armour; 2) the shape of the dorsal wall; 3) the absence of the dorsal median ridge; 4) the shape of the anterolateral corner of AVL; 5) the shape and proportions of the Prm. *B. taylori* differs from *B. panderi* in its 1) larger size; 2) proportions of the AMD; 3) shape of the CD1. *B. paradoxa* (Agassiz, 1845) from the Scaat Craig Beds differs from *B. panderi* in the shape of Prm, shape and proportions of Nu, AMD and ADL, position of the tergal angle, the character of the ornamentation. (For the comparison of *B. panderi* with *B. traudscholdi* see the description of the latter).

Bothriolepis traudscholdi Jaekel, 1927 (Figs 13-22)

Bothriolepis panderi Lahusen, 1880: 137, taf. 2, figs 2-4. — Trautschold 1880: 172 (fig.). — Gross 1932: 25 (*p.p.*); 1933: 39, 40, taf. 4, fig. 6; abb. 21; 1941: abb. 10B, C, 11G, H, 26H-K, 27D, E. — Stensiö 1948: 424; text-fig. 229A, 231 [non text-fig. 230]. — Watson 1961: text-fig. 1. — Obruchev 1964: pl. 6, fig. 6.

Bothriolepis tremdscholdi – Jaekel 1927: 869, abb. 21.

Bothriolepis traudscholdi Jaekel, 1927: 932, abb. 60. — Gross 1932: 25; 1933: 40 (*nomen negatum*).

TYPE SPECIMEN. — Jaekel (1927) proposed a new species of *Bothriolepis* for a head-shield collected by Trautschold (1880, shown also by Gross in 1933) at Syas' River not far from Stolbovo village (Russia), said to be held in the Museum of Breslau (now Wroclaw in Poland). Part of the Trautschold collection is held in this museum, but the specimen shown by Jaekel cannot be located (pers. comm. A. Ivanov). Therefore, I propose here the head-shield PIN 330/33, collected by J. Eglons in 1937 at the type locality and illustrated by Obruchev (1964: pl. 6, fig. 6), as a neotype of *Bothriolepis traudscholdi*.

MATERIAL EXAMINED. — PIN 330/39, 41-75, 77-98, 100-107, 110-128, 29/1, 2, articulated head-shields and disarticulated plates of the skull roof and trunk armour; PIN 2917/41-46, articulated head-shields and anterior divisions of the trunk armour; LDM 63/1-33, 35-51, 53-230, 241-396, IEC LP 12/1-5, disarticulated plates of the skull roof and trunk armour; IEC LP 12/6, articulated plates of the dorsal trunk armour; NHM P.34465, sandstone block with 20 bones, including articulated head-shields; RSM 1902.72.4, AMD, 1902.72.6, PMD. Disarticulated plates of the head-shield LDM 71/18, Prm, 71/51, Nu, 71/52, La; disarticulated plates of the trunk armour LDM 71/2, 34, 36, 38, 39, 42, 45, 47, 50, 87, 89-92, 97, 161 and plates of the pectoral fin LDM 71/54-57, 62, 101, 125, 131, 132 are tentatively referred to this species.

LOCALITIES AND HORIZON. — The type locality is an outcrop of dark red-coloured sandstone with thin layers of clayey siltstone, multicolored marl and clay, on the right bank of the Syas' River near Stolbovo village, Russia. Other material comes from the outcrops at Syas' River near Yukhora village, not far from Stolbovo, and exposure of the dolomites at the left

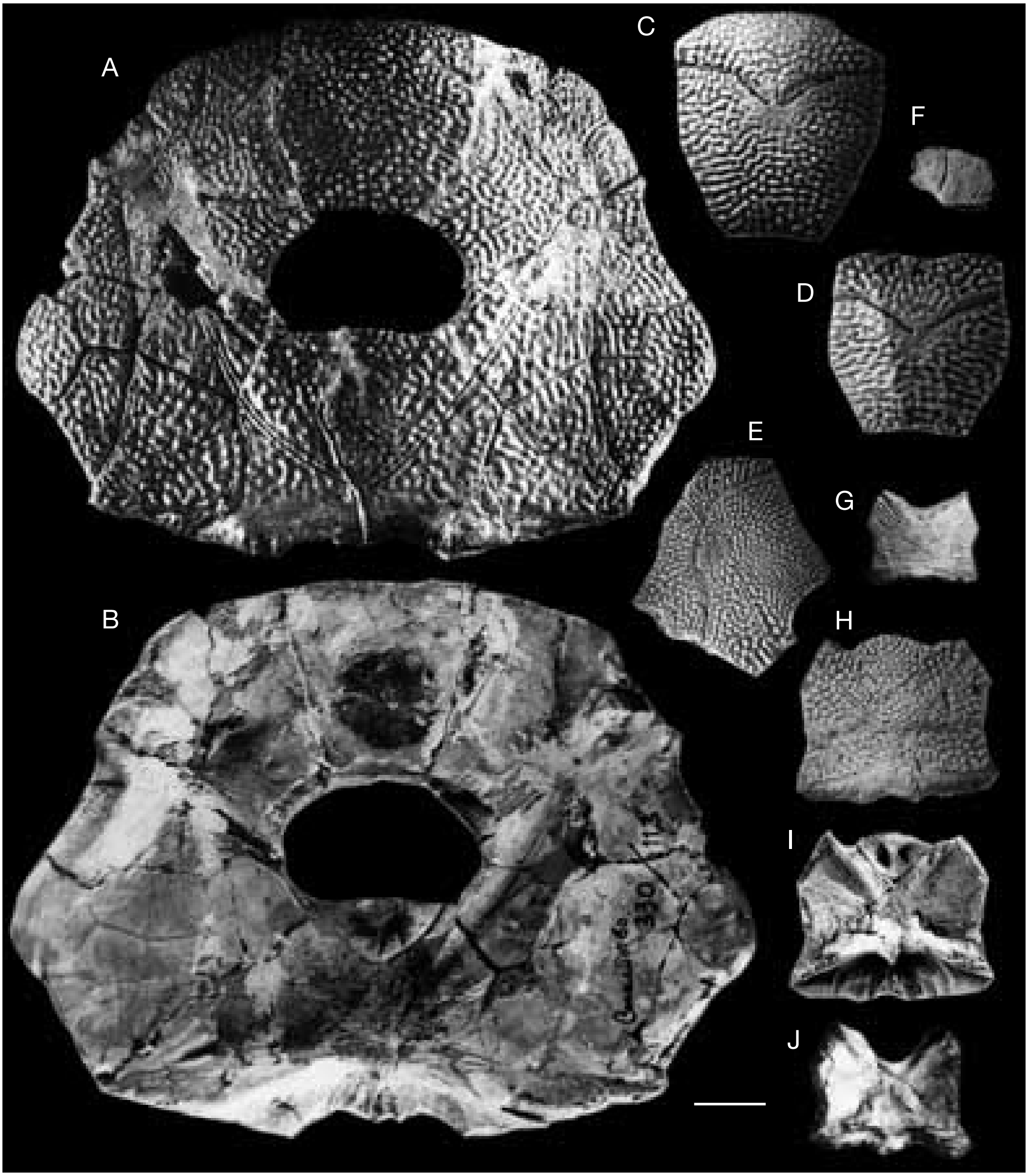

FIG. 13. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**, **B**, head-shield PIN 330/113 in dorsal and visceral views; **C**, Prm PIN 330/126 in dorsal view; **D**, Prm PIN 330/127 in dorsal view; **E**, La PIN 330/124 in dorsal view; **F**, Pn LDM 63/138 in dorsal view; **G**, Nu LDM 63/149 in dorsal view; **H**, **I**, Nu and Pp PIN 330/42 in dorsal and visceral views; **J**, Nu LDM 63/156 in visceral view. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate. Scale bar: 10 mm.

bank of the Gauja River not far from Vidaga village, Latvia. All Russian material comes from the Frasnian Dubnik Formation. The Latvian material comes from the Altovo Member of the Daugava Formation. A possible new form of *Bothriolepis* from the Matusevich Formation of Severnaya Zemlya seems to be closely related to *Bothriolepis traudscholdi* from the Main Devonian Field (Lukševičs 1999).

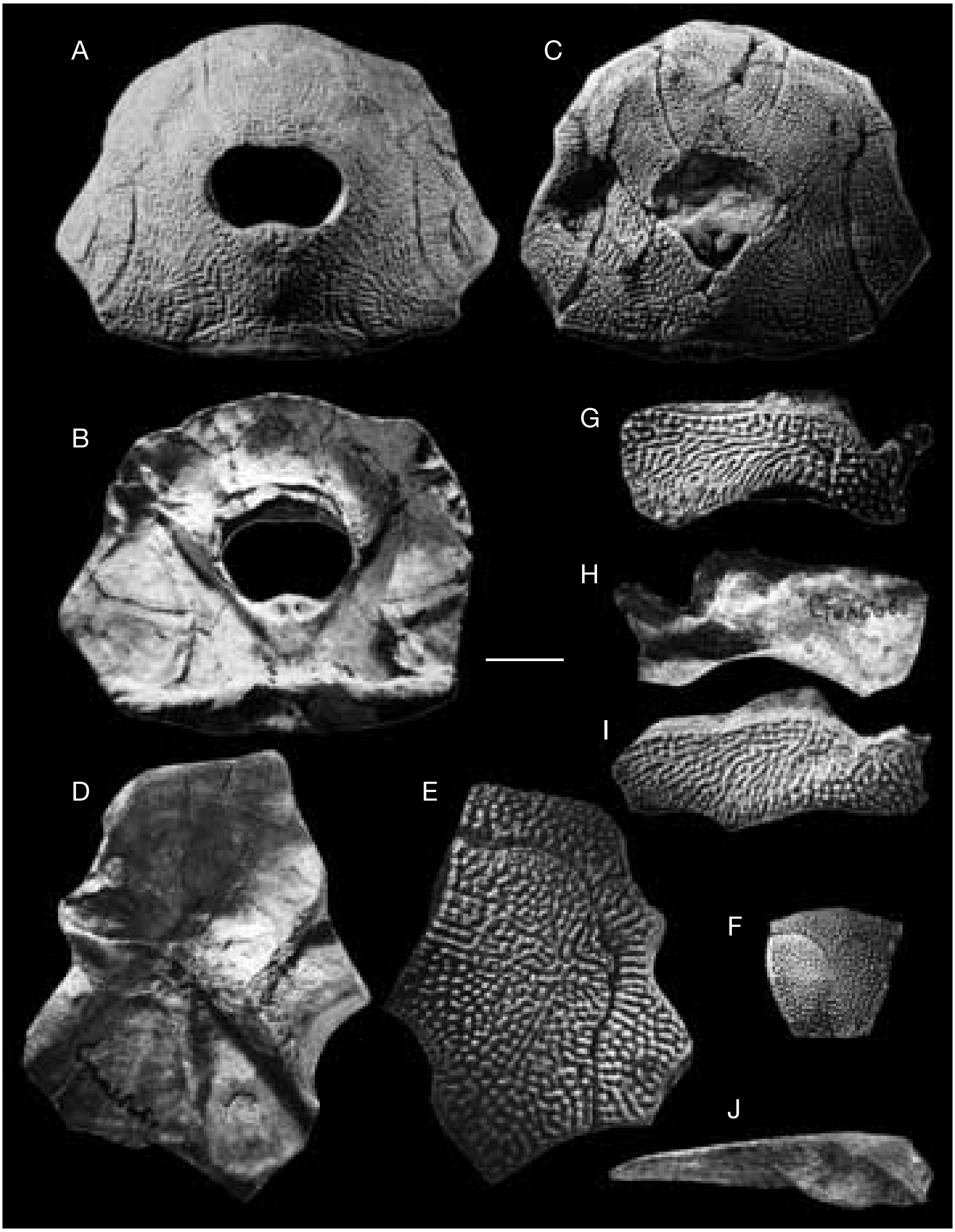

FIG. 14. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**, **B**, head-shield PIN 330/117 in dorsal and visceral views; **C**, head-shield PIN 330/125 in dorsal view; **D**, La PIN 330/115 in visceral view; **E**, La PIN 330/112 in dorsal view; **F**, Prm PIN 330/46 in dorsal view; **G**, **H**, Sm PIN 330/116 in lateral and visceral views; **I**, **J**, Sm PIN 330/114 in lateral and dorsal view. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **La**, lateral plate; **Prm**, premedian plate; **Sm**, submarginal plate. Scale bar: 10 mm.

DIAGNOSIS. — Rather large *Bothriolepis* with a median dorsal armour length of at least 140 mm. Head-shield of moderate width, B/L index 133, with strongly convex anterior margin shorter than posterior margin. Orbital fenestra long. Preorbital recess of simple type. Nu moderately broad with B/L index of

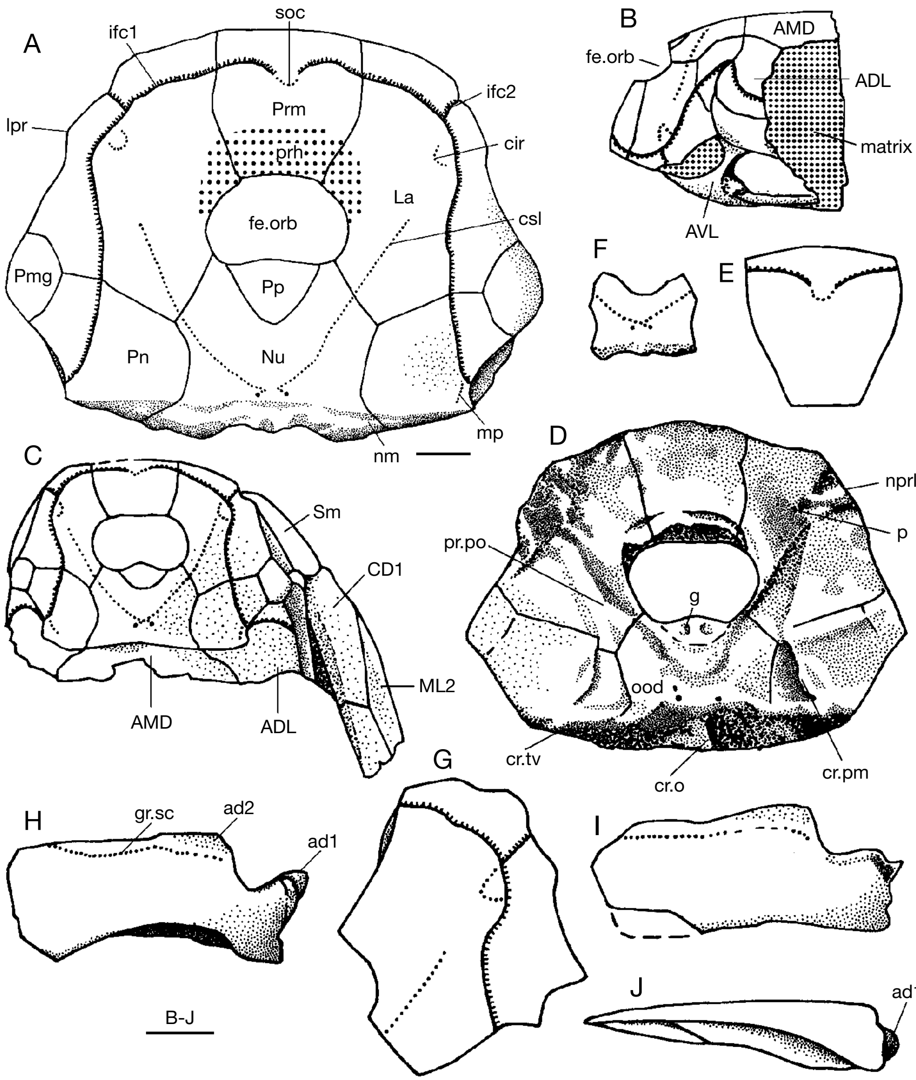

FIG. 15. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**, head-shield PIN 330/113 in dorsal view; **B**, head-shield, anterior part of AMD, left ADL, AVL, CD1 and CV1 PIN 2917/45 in lateral view; **C**, head-shield, anterior part of AMD, both ADL, right AVL and proximal segment of the pectoral fin PIN 2917/43 in dorsal view; **D**, head-shield PIN 330/117 in visceral view; **E**, Prm PIN 330/118; **F**, Nu LDM 63/149; **G**, La LDM 63/131; **H-J**, submarginal plates; **H**, PIN 330/116 in lateral view; **I**, **J**, PIN 330/114 in lateral and ventral views. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD1**, dorsal central plate 1; **CV1**, ventral central plate 1; **La**, lateral plate; **ML2**, lateral marginal plate 2; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **Sm**, submarginal plate; **ad1**, anterior articular process; **ad2**, posterior articular process; **cir**, semicircular pit-line groove; **cr.o**, median occipital crista of head-shield; **cr.pm**, paramarginal crista of head-shield; **cr.tv**, transverse nuchal crista of head-shield; **csl**, central sensory line groove; **fe.orb**, orbital fenestra; **g**, paired pits on Pp; **gr.sc**, groove, possible for sensory canal; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **lpr**, lateral process of head-shield; **mp**, middle pit-line groove; **nm**, obtected nuchal area; **nprl**, prelateral notch; **ood**, otico-occipital depression; **p**, lateral pit; **prh**, preorbital recess; **pr.po**, antero-lateral corner of otico-occipital depression; **soc**, anterior section of the supraorbital sensory line. Scale bars: 10 mm.

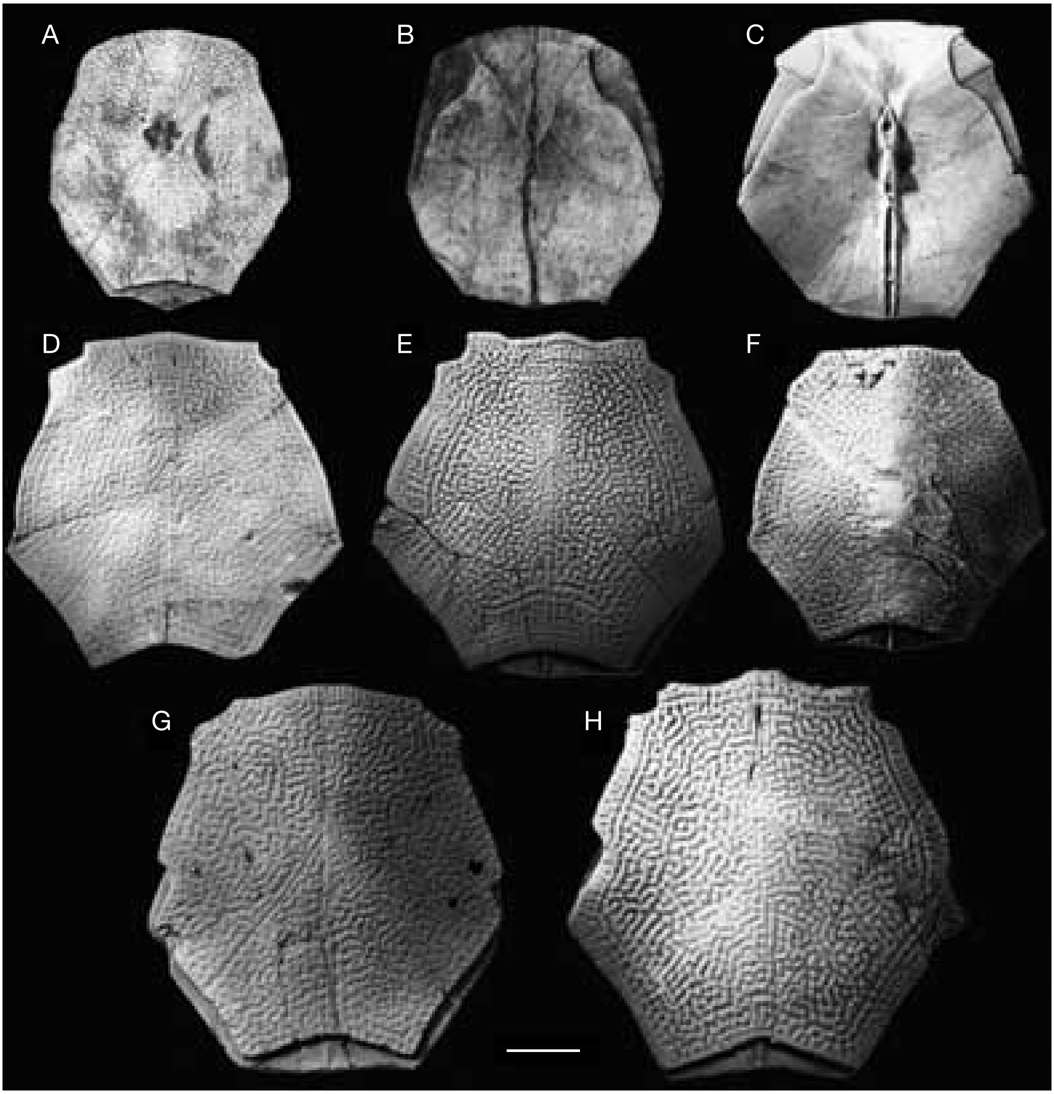

FIG. 16. — *Bothriolepis traudscholdi* Jaekel, 1927, AMD; **A**, **D**-**H**, dorsal views; **A**, LDM 63/41; **D**, PIN 330/56; **E**, PIN 330/55; **F**, PIN 330/52; **G**, LDM 63/37; **H**, PIN 330/53; **B**, **C**, visceral views; **B**, LDM 63/44; **C**, PIN 330/57. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviation: **AMD**, anterior median dorsal plate. Scale bar: 10 mm.

about 81; it is broadest across the postero-lateral corners. AMD moderately broad, B/L index about 94. The anterior margin 1.9 time shorter than the maximum width of the plate. Postnuchal notch pronounced, with very strong anterolateral corners. Median dorsal ridge weakly developed and practically absent in large individuals. PMD is relatively broad with B/L index about 104. Postnuchal ornamented corner of the ADL is sharp, long and narrow. Axillary fenestra longer than high. Proximal segment of the pectoral fin is slender, about 4.4 times as long as broad; it bears separate relatively small lateral and mesial spines, which are almost similar to the tubercles, composing the ornamentation. The point contact between MM1 and CV2 of pectoral fin results in separation of CV1 from MM2. The ornamentation is fine-meshed in very small individuals, typically tubercular in medium-sized individuals and has mixed character in large individuals, consisting of tubercles and anastomosing ridges on the skull roof and plates of the trunk armour.

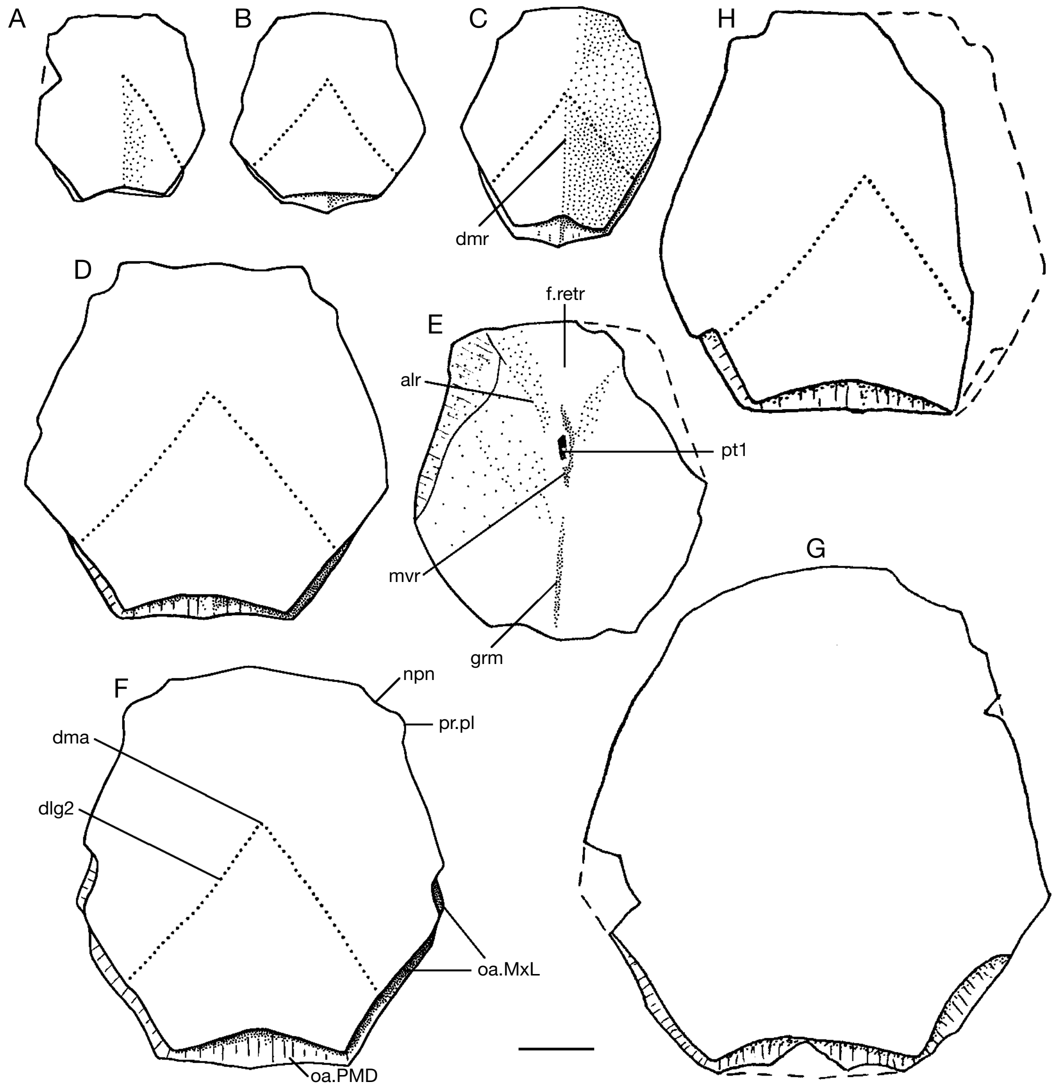

FIG. 17. — *Bothriolepis traudscholdi* Jaekel, 1937, AMD; **A**-**D**, **F**-**H**, dorsal views; **A**, LDM 63/18; **B**, LDM 63/24; **C**, LDM 63/7; **D**, PIN 330/52; **F**, LDM 63/67; **G**, LDM 63/30; **H**, LDM 71/34; **E**, visceral view, LDM 63/13. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Left bank of Gauja River near Vidaga village, Latvia. Kranciems Member of the Daugava Formation. Abbreviations: **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **alr**, postlevator thickening; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **dmr**, dorsal median ridge; **f.retr**, levator fossa; **grm**, ventral median groove; **mvr**, median ventral ridge; **npn**, postnuchal notch; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **pr.pl**, external postlevator process; **pt1**, anterior ventral pit. Scale bar: 10 mm.

DESCRIPTION

This species is well-represented at the type locality by many disarticulated plates, as well as some articulated skulls and trunk shields, which are usually well-preserved. Almost all specimens from the Vidaga site are incomplete and usually deformed, in many cases preserved only as an impressions. Most are from small or well-grown individuals of moderate size, but there are also some quite large specimens.

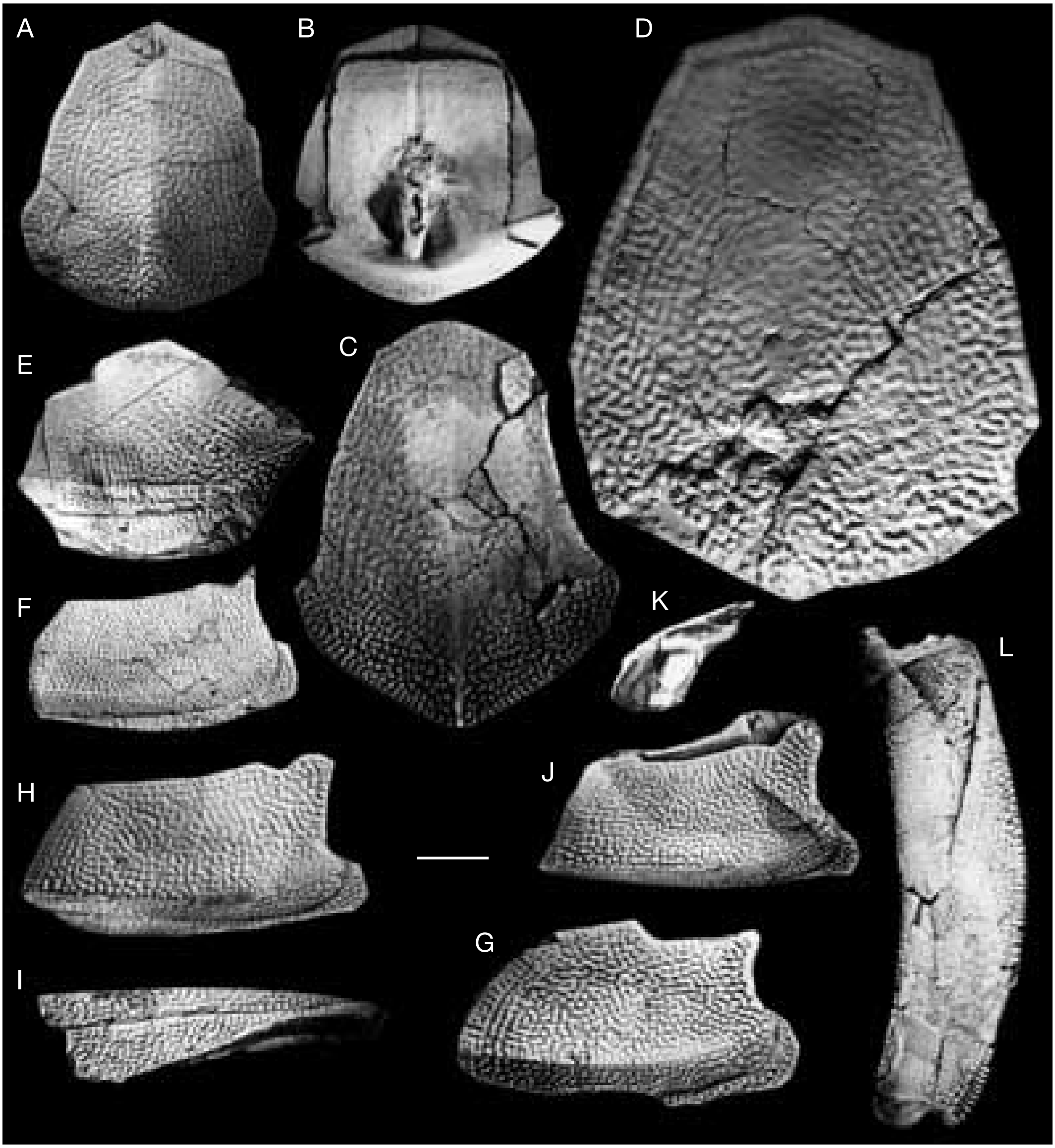

FIG. 18. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**, PMD PIN 330/47 in dorsal view; **B**, PMD PIN 330/58 in visceral view; **C**, PMD PIN 330/48 in dorsal view; **D**, PMD LDM 63/58 in dorsal view; **E**, MxL PIN 330/94 in dorsal view; **F**, ADL LDM 63/98 in dorsal view; **G**, ADL PIN 330/86 in dorsal view; **H**, **I**, ADL PIN 330/87 in dorsal and lateral views; **J**, **K**, ADL PIN 330/98 in dorsal and anterior views; **L**, proximal segment of the pectoral fin PIN 330/68 in ventral view. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate. Scale bar: 10 mm.

The length of the head shield reaches about 75 mm, the dorsal length of the trunk armour is estimated at least about 140 mm. The head shield (Figs 13A, B; 14A-C; 15A-D) has B/L index is of 130-140 (of average 133, n = 4). It is strongly vaulted both rostrocaudally and transversely in small individuals, but is flat in the well-grown individuals. There are well-defined anterolateral

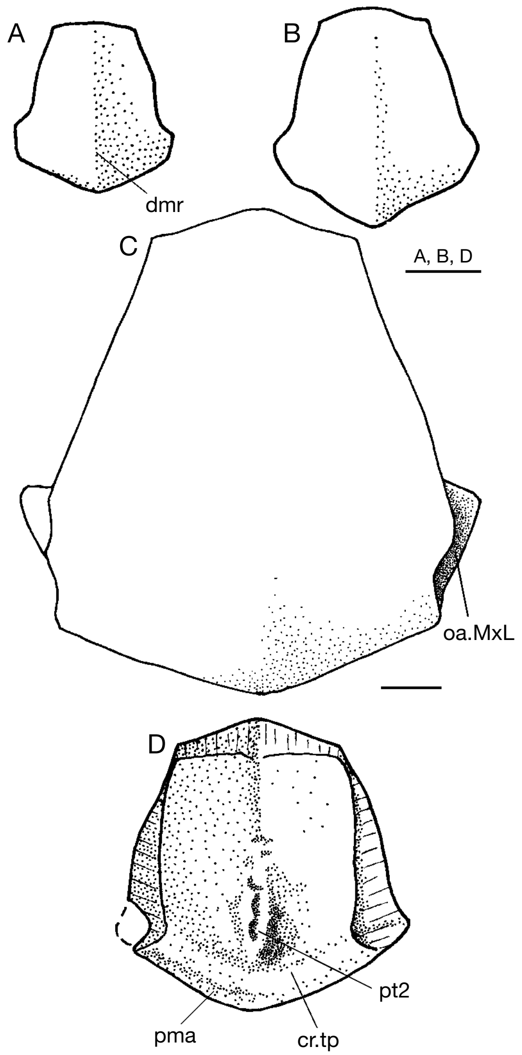

FIG. 19. — *Bothriolepis traudscholdi* Jaekel, 1927, PMD; **A**-**C**, dorsal views; **A**, LDM 63/76; **B**, LDM 63/71; **C**, LDM 63/58; **D**, visceral view, PIN 330/50. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **cr.tp**, crista transversalis interna posterior; **dmr**, dorsal median ridge; **oa.MxL**, area overlapped by MxL; **pma**, posterior marginal area of PMD; **pt2**, posterior ventral pit. Scale bars: 10 mm.

corners (alc) and a deep prelateral notch (nprl). The obtected nuchal area (nm) is of moderate width, broadest on the Nu, and usually with well-defined lateral and median processes. The orbital fenestra is moderately large, long, with a B/L index about 150-167, 156 on the average.

The visceral skull surface (Figs 13B; 14B; 15D) shows the broad otico-occipital depression (ood), which is well-defined by the paramarginal cristae (cr.pm). The antero-lateral corner of otico-occipital depression (pr.po) is narrow in its base, postero-lateral corner extends laterally not over the middle of the Pn's posterior margin. The transverse lateral groove is moderately broad and clearly defined. The small, deep lateral pit (p) is situated closer to a prelateral notch than to the orbital edge of La. The attachment areas for the Prl and Sm on the La differs slightly from that of *B. canadensis* (e.g., Stensiö 1948: fig. 12) in that the overlap area for Prl is only slightly visible from the ventral side, as in *Bothriolepis* sp. from Gogo or *B. portalensis* (see Young 1988: fig 66B, D). The median occipital crista (cr.o) is slightly defined, often it consists of several radially arranged small ridges. The transverse nuchal crista is prominent, with the median part extending anteriorly. The median ridge (mr) sharing the moderately deep paired pits (g) of Pp is low.

The Prm is relatively broad, B/L index 90-110, 99 on the average. Usually it is broadest somewhat posteriorly the infraorbital sensory groove. The rostral angle (ac) usually is absent. The shape of the rostral margin is variable, often it is convex. The orbital margin is gently convex and well shorter than the rostral margin. The nasal notch (pnn) on the orbital margin is not well-defined. The anterior section of the supraorbital sensory line (soc) usually is clearly defined.

The La is moderately broad with L/B index of 130-143, 134 on the average. The rostral margin is almost straight, the antero-median and antero-lateral corners are well-defined. The infraorbital sensory groove crosses the plate in its anterior part not far from the orbital and lateral margins. The central sensory line groove (csl) usually is finished at the level of the anterior margin of the orbital fenestra.

The Pp is broad both in small and moderate-sized individuals, L/B index varies from 57 to 71. The anterior margin remains convex with increasing size of individuals.

The Nu is moderately broad with a L/B index 71-90, 81 on the average. The anterior division of the lateral margin usually is almost straight and well shorter than the posterior division. The shape of the posterior margin is variable, sometimes it is strongly concave, often bears the posterior process (mppr). The central sensory line groove is clearly distinct. Usually there are short supraoccipital grooves (socc), which terminate little in front of the obtected nuchal area at the external openings for the endolymphatic ducts (d.end). Postorbital crista (cr.pto) on the visceral surface is moderately high.
The Pn is moderately long, L/B index 71-103, 88 on the average. Sometimes (in PIN 330/115) it bears short middle pit-line (mp). The lateral division of the Pn is moderately broad and is composing 45-68% of the general breadth of a plate.
The Pmg is relatively broad with lateral margins longer than the median margins.
The submarginal (extralateral) plate (Figs 14E-J; 15H-J) is comparatively long with L/B index about 220-270. The dorsal margin has a prominent anterodorsal process (ad1) and a narrow posterior attachment area for the skull. The posterior margin is almost straight, the ventral margin is weakly to strongly concave. A well-marked lateral notch is rather deep separating the plate into a short thick anterior division and more thin posterior division. The specimen PIN 330/116 (Figs 14G; 15H) shows a groove (gr.sc) running along the dorsal margin of the ornamented part of the plate in its posterior division, which is similar to that of *Bothriolepis obrutschewi* (pers. obs.) and *B. macphersoni* and has the character of a sensory groove.
The trunk armour in individuals of moderate size is known from a large amount of disarticulated plates and several anterior parts of articulated armours, sometimes with articulated pectoral fins, of small individuals.
The trunk-armour in individuals of small size as it is remained in specimens PIN 2917/41-46 is moderately broad, B/L index 86. It is relatively low with moderately high dorsal wall. The maximum length of the dorsal wall, probably, is about 140 mm. The median dorsal ridge is well-defined in small individuals, weakly developed in medium-sized individuals and represented

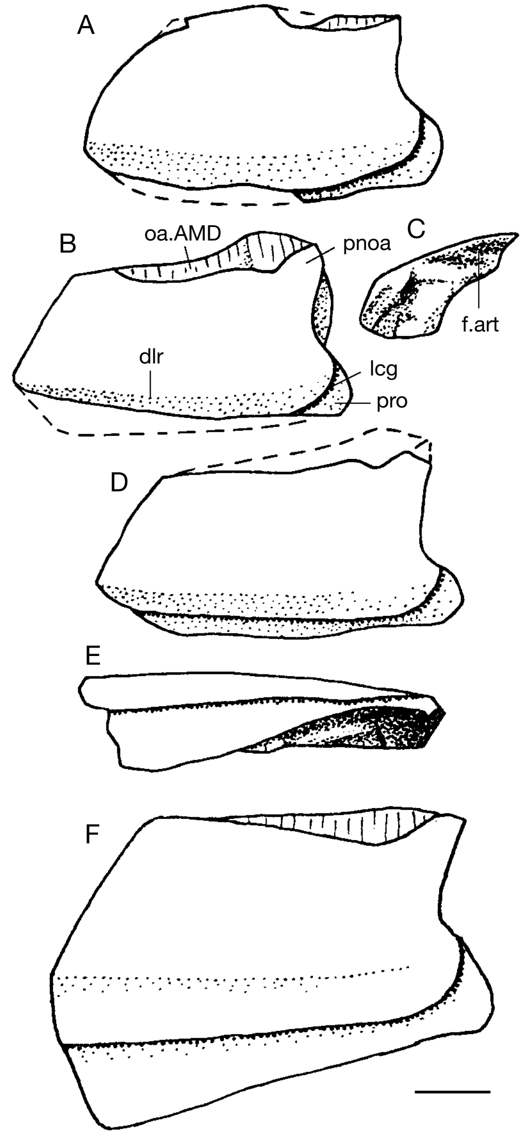

Fig. 20. — *Bothriolepis traudscholdi* Jaekel, 1927, ADL; **A**, PIN 330/86 in dorsal view; **B**, **C**, PIN 330/98 in dorsal and anterior views; **D**, **E**, PIN 330/87 in dorsal and lateral views; **F**, LDM 71/45 in dorsal view, somewhat flattened; **A**-**E**, right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation; **F**, left bank of Gauja River near Vidaga village, Latvia. Kranciems Member of the Daugava Formation. Abbreviation: **ADL**, anterior dorso-lateral plate. Scale bar: 10 mm.

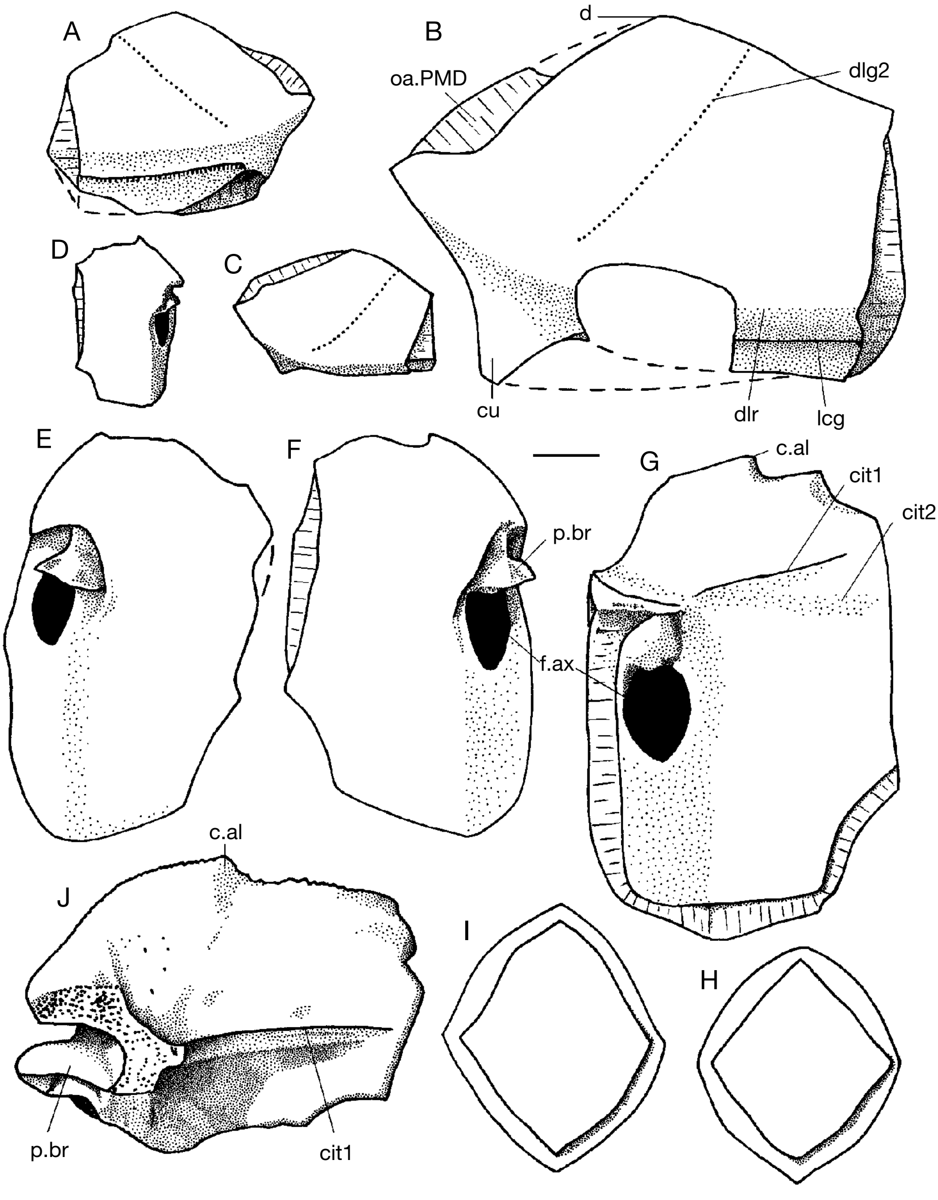

FIG. 21. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**-**C**, MxL; **A**, PIN 330/99; **B**, LDM 63/82; **C**, LDM 63/85; **D**-**G**, AVL; **D**, LDM 63/109 in ventral view; **E**, PIN 330/64 in ventral view; **F**, LDM 63/107 in ventral view; **G**, LDM 63/108 in visceral view; **H**, **I**, MV in ventral view; **H**, LDM 63/122; **I**, LDM 63/123. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation; **J**, *Bothriolepis panderi* Lahusen, 1880, anterior part of the AVL plate LDM 63/338 in visceral view. Right bank of Syas' River near Montsevo village, Russia. Snetnaya Gora Beds. Abbreviations: **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **c.al**, antero-lateral corner of subcephalic division; **cit1**, crista transversalis interna anterior; **cit2**, transverse thickening on the visceral surface of AVL; **cu**, postero-ventral ornamented corner; **d**, dorsal corner; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge of trunk armour; **f.ax**, axillary foramen; **lcg**, main lateral line groove; **oa.PMD**, area overlapped by PMD; **p.br**, processus brachialis. Scale bar: 10 mm.

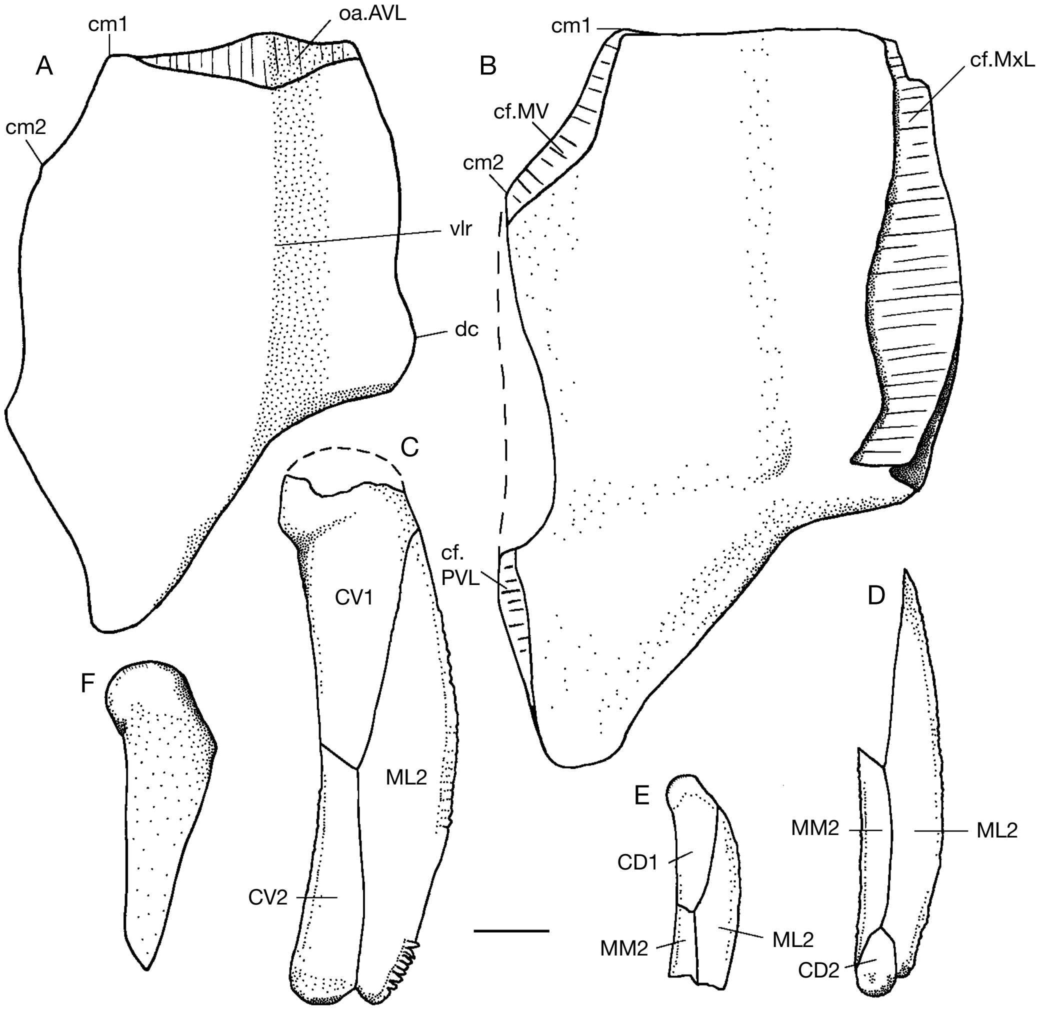

FIG. 22. — *Bothriolepis traudscholdi* Jaekel, 1927; **A**, **B**, PVL; **A**, LDM 63/114 in ventral view; **B**, LDM 63/113 in visceral view; **C**, proximal segment of the pectoral fin PIN 330/68 in ventral view; **D**, part of the proximal segment of the pectoral fin LDM 63/132 in dorsal view; **E**, part of the proximal segment of the pectoral fin LDM 63/139 in dorsal view; **F**, CV1 LDM 63/158 in ventral view. Right bank of Syas' River near Stolbovo village, Russia. Dubnik Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **CD1**, dorsal central plate 1; **CD2**, dorsal central plate 2; **CV1**, ventral central plate 1; **CV2**, ventral central plate 2; **ML2**, lateral marginal plate 2; **MM2**, mesial marginal plate 2; **MV**, median ventral plate; **MxL**, mixilateral plate; **PVL**, posterior ventro lateral plate; **cf.MV**, area overlapping MV; **cf.MxL**, area overlapping MxL; **cf.PVL**, area overlapping PVL; **cm1**, anteromesial corner of ventral lamina of PVL; **cm2**, middle corner of ventral lamina of PVL; **dc**, dorsal corner of lateral lamina of PVL; **oa.AVL**, area overlapped by AVL; **vlr**, ventro-lateral ridge. Scale bar: 10 mm.

only in its posterior part in large individuals. The dorso-lateral and ventro-lateral ridges are well-marked in small individuals and are rounded in large individuals.

The AMD is moderately broad, B/L index varying from 84 to 105, 94 on the average. The anterior margin is generally convex, sometimes somewhat wavelike in shape, relatively long. The anterior margin is usually 1.1 time longer than the posterior margin. The antero-lateral and lateral corners are well-defined. The posterior division of the lateral margin is 1.5-1.9 time shorter than the anterior division. The tergal angle (dma) is situated slightly posteriorly the anterior third of the plate. The median dorsal ridge (dmr) is well-developed on the small 17-23 mm long plates; it is slightly defined behind the tergal angle on the plates of moderate size with the length 24-25 mm. More large plates with the length over 26 mm have no median dorsal ridge. The postnuchal notch (npn) is broad and shallow, the postlevator process (pr.pl) is well-defined. The anterior oblique dorsal sensory line groove (dlg1) is gently defined only in smallest specimen LDM 63/17 which is 17 mm long. The posterior oblique dorsal sensory line groove (dlg2) is clearly defined also on the plates of very large individuals. Specimen LDM 63/18 (Fig. 17A) shows the posterior oblique dorsal sensory line groove developed only on the left lamina of the plate. Overlap areas for ADL and MxL mostly are normally developed as usually in *Bothriolepis*, but in LDM 63/30 (Fig. 17G), 63/8, and 71/34 (Fig. 17H) sutural connection of AMD with MxL is of *Remigolepis* type. The antero-lateral margins in LDM 63/37 (Fig. 16G) and PIN 330/53 (Fig. 16H) are partly overlapped by ADL, in 63/14 such overlapped area is developed on the right side (the left side is broken).

The visceral surface of the AMD (Figs 16B, C; 17E) shows a moderately broad levator fossa (f.retr), which is limited by the low postlevator thickenings (alr). The supranuchal area (sna) is clearly seen, but relatively narrow. The median ventral ridge (mvr) and the median ventral groove (grm) are developed similar as in other *Bothriolepis*.

The PMD is variable, usually broad, sometimes very broad (in LDM 63/65), or relatively narrow (in PIN 330/47 and PIN 330/48), B/L index varies from 91 to 112, 104 on the average. Whether the differences in proportions of the plate reflects sexual dimorphism or even presence of two species within the material, is very hard to say, because in other respects narrow and broad plates does not differ. The PMD is anteriorly almost flat and arched in the posterior part. The dorsal median ridge is well-marked along the whole plates in small individuals and in the posterior half of PMD in medium-sized and large individuals. The anterior margin is 1.7 to 2.2 times as long as the total width of the plate, it is variable in its shape, usually without distinct anterior corner. The posterior margin usually has rounded, sometimes concave or pointed posterior median corner. The lateral margins of the plate generally overlapping the MxL, but in LDM 63/58 there are narrow areas along the lateral process of the PMD overlapped by the MxL (Fig. 19C).

On the visceral surface (Figs 18B; 19D), the ventral median groove (grm) is clearly shown also in small specimens, the ventral median ridge (mvr) is low with shallow posterior ventral pit, which is situated in posterior half of the plate. Posterior marginal area (pma) is relatively short.

The ADL (Figs 18F-K; 20) has relatively elongated dorsal lamina. The posterior margin of the lateral lamina is approximately equal in breadth to the posterior margin of the dorsal lamina. The lateral lamina is about three times as long as it is deep. The dorso-lateral ridge is well-marked in the posterior part of the plate. The postnuchal ornamented corner (pnoa) resembles that of *B. ciecere*; in large specimens it is more broad. Notch behind it is poorly formed. The dorsal margin of the plate bears an overlap area for the AMD usually along the whole of its length, but in specimens PIN 330/86 (Figs 18G; 20A) and 330/98 (Figs 18J; 20B) the ADL overlaps the AMD by its posterior half. Processus obstans is well-developed, with high articulation lamina. The articular fossa for the exoskeletal cervical joint (f.art) is clearly demarcated by well-developed supra- and infra-articular cristae (crs, cri) (Figs 18K; 20C).

The MxL (Figs 18E; 21A-C) has a comparatively low lateral lamina which is more than 3 times as long as it is deep, and a relatively broad dorsal lamina about 1.6-1.7 time as long as it is broad. The anterior margin concave or wavy. Dorsal and lateral laminae meet at an angle of about 113°. Dorsolateral ridge is well-marked, in large specimens it is rounded. Overlap area for the AMD in specimen PIN 330/94 (Fig. 18E) is

restricted to half the length of the antero-dorsal margin, as in *Remigolepis*.
The AVL (Fig. 21D-G) is comparatively broad, the ventral lamina is 1.5-1.8 time as long as it is broad. The subcephalic division comprises 20-25% of the total length of a ventral lamina. The ventral lamina 2.1-3 times as broad as the lateral lamina high. The lateral lamina is low, 3-3.8 times as long as it is high. The ventro-lateral ridge is well-defined, sometimes rounded off. The axillary foramen (f.ax) is rather large and elongated. The visceral surface of the AVL shows the high transverse anterior crista (cit1) running antero-mesially very close to the broad transverse thickening (cit2).
The PVL (Fig. 22A, B) is of moderate breadth, the ventral lamina is 2-2.5 times as long as it is broad. The subanal division is relatively broad and long, it occupies about 30-36% of the total PVL length. The lateral lamina is moderately high, 1.8-2 times long as it is high. The ventral lamina 1.2-1.3 time as broad as the lateral lamina high. The ventro-lateral ridge (vlr) is well-defined.
The pectoral fin is represented by many disarticulated bones, and four specimens showing articulated plates of the proximal segment (Figs 18L; 22C-F). The comparatively slender proximal segment bears separate relatively small lateral and dorsally directed mesial spines; the latter are usually similar to the tubercles composing the ornamentation. The proximal segment is 4.1-4.6 times as long as it is broad. The CD1 is of moderate size with L/B index varying from 2.6 to 3.1 (2.8 on the average, n = 4). The CV1 is relatively more elongated and have the L/B index about 2.8-3.6 (3.2 on the average). The ML2 is 4.8-5.7 (5.2 on the average) times as long as it is broad.
The ornamentation is fine-meshed reticulate in very small individuals, e.g. 18.9 mm long PMD plate LDM 63/270, and typically tubercular in general in medium-sized and quite large individuals, becoming coarser and sparser. It consists of coarse tubercles and anastomosing ridges of fused tubercles on the head shield. The tubercles cover usually almost all the surface of the Prm, Pm, partly La, Pn and Pp. The ornament on the Sm consists of ridges and tubercles. The ornament on the plates of the trunk armour is typically tubercular in general, but retains its very variable character. Some plates have all possible patterns of the ornament on their surface, especially in large specimens. The ornamentation of the pectoral appendage is also variable. It is reticulate in general, on the CD1 and dorsal lamina of the ML2 the network ridges bear tubercles in the points of anastomoses only along the lateral margin, more well-developed in proximal part. The ornament on the ventral side of the pectoral appendage is reticular in general.

Remarks

Bothriolepis traudscholdi was illustrated by Jaekel (1927) as a new species from Syas' River which differs from *B. panderi*, but he did not provide its description. This species was named as "*Bothriolepis tremdscholdi* n. sp." in explanation to abb. 21 and "*B. traudscholdi* Jkl." in abb. 60 of Jaekel's (1927) paper; both were regarded to be misprintings by Gross (1933) and he incorrectly changed the original spelling into *B. trautscholdi* in a list of synonyms to *B. panderi*. However, in the catalogue of antiarchs, Gross (1932) have used the name *B. traudscholdi*, but did not clearly define this action. Therefore, acting as a first reviser, I propose here to choose the name *Bothriolepis traudscholdi* as a valid name for this taxon. Gross (1933) mentioned *B. traudscholdi* as a synonymous to *B. panderi*, but without any further comments. Stensiö (1948) agreed with Gross (1933) and provided description of *B. panderi* including material, which I suppose to be attributable to *B. traudscholdi*. The description of *B. traudscholdi* here is based on extensive material from the type locality, gathered by J. Eglons & D. Obruchev in 1937, L. Lyarskaja in 1974, and author together with A. Ivanov in 1988. This material was never described in details, being only mentioned as belonging to *B. panderi* (e.g., Obruchev 1964). Specimens from Vidaga site at Gauja River were collected by Lyarskaja in 1978 and the author together with Lyarskaja in 1983.

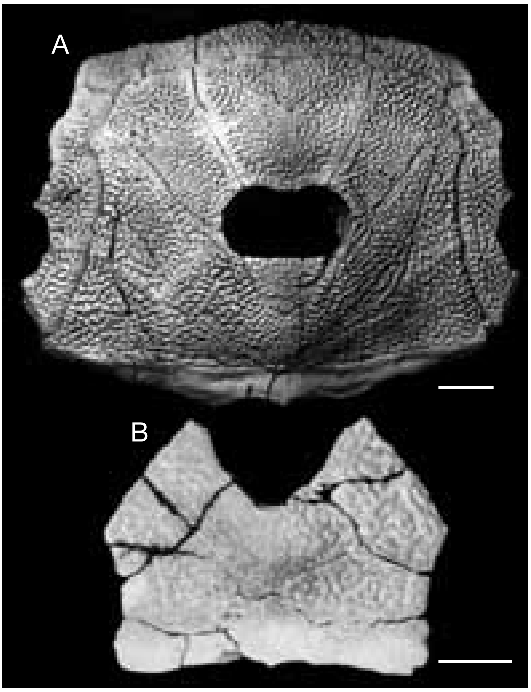

FIG. 23. — *Bothriolepis maxima* Gross, 1933; **A**, head-shield LDM 99/1 in dorsal view; **B**, Nu LDM 99/6. Right bank of Imula River near Kalnarāji hamlet, Latvia. Ogre Formation. Abbreviation: **Nu**, nuchal plate. Scale bars: 20 mm.

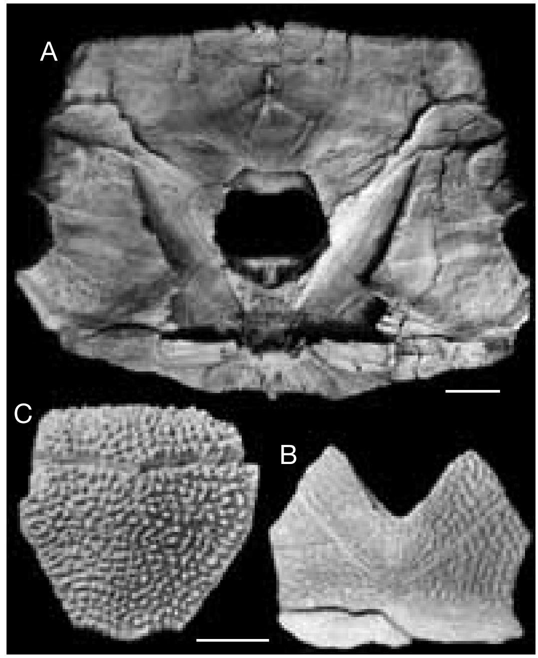

FIG. 24. — *Bothriolepis maxima* Gross, 1933; **A**, head-shield LDM 99/1 in visceral view; **B**, Nu LDM 99/5; **C**, Prm LDM 99/2. Right bank of Imula River near Kalnarāji hamlet, Latvia. Ogre Formation. Abbreviation: **Nu**, nuchal plate; **Prm**, premedian plate. Scale bars: 20 mm.

DISCUSSION

Bothriolepis traudscholdi resembles *B. panderi* by several features: 1) the general shape of the head-shield; 2) proportions of the Pn and Pmg; 3) general proportions of the trunk armour; 4) weak development of the dorsal median ridge; 5) position of the tergal angle; 6) proportions of the ADL; 7) proportions of the slender pectoral fin. Nevertheless, *B. traudscholdi* differs considerably from *B. panderi* in its 1) comparatively narrower head-shield; 2) more vaulted anterior part of the head-shield; 3) larger and longer orbital fenestra; 4) shape and proportions of the Prm and Nu; 5) more anterior extent of the central sensory line groove; 6) more broad AMD; 7) shorter anterior margin of the AMD; 8) shape of the postnuchal ornamented corner of the ADL; 9) longer subcephalic division of the AVL.

B. traudscholdi differs well from *B. obrutschewi* in its strongly larger size, shape and proportions of the Prm and Nu, relative length of the anterior margin of the AMD, shape and proportions of the PMD, ADL and MxL, as well as more elongated pectoral fin. *B. traudscholdi* can be distinguished readily from *B. cellulosa* by larger size, shape and proportions of the La and Nu, relative length of the anterior margin of the AMD, shape and proportions of the AMD, PMD and MxL, more elongated pectoral fin and tubercular rather than reticular ornamentation.

Bothriolepis maxima Gross, 1933
(Figs 23-28)

Bothriolepis maxima – Gross 1932: 25 (*nomen nudum*).

Bothriolepis maxima Gross, 1933: 41-43; taf. 5, fig. 14.

HOLOTYPE. — The head-shield f124 Geologisch-Paläontologische Institut und Museum der Universität Berlin.

MATERIAL EXAMINED. — LDM 43/675, 99/1, 84/67, three articulated head-shields; PIN 1652/2, articulated head-shield and dorsal trunk armour; LDM 15/20, 23, 25-31, 125; 43/676-710, 43/712-721; 84/1-14, 17-19, 21-30, 33-38, 40-47, 66; 87/1, 3, 4, 7-9, 11, 13, 14, 18; 99/2-44; PIN 89/3; 1491/87, 96-98; 1737/62-64; 1767/61; 2917/21,24-33, 35, 37-39, 41-44, 51-53, disarticulated plates of the head-shield, trunk armour and pectoral fin; LUGM 872, 1105: 2 MV.

LOCALITIES AND HORIZON. — The type locality of *Bothriolepis maxima* is the outcrop of the Ogre Formation sandstones at Imula River not far from Lankserde hamlet, Latvia; Ogre Formation. Other material came from the other outcrops at Imula River near Kalnarāji hamlet and Vītiņi hamlet, exposure and caves Velna Ala at Abava River, outcrops along Ogre River, outcrop at Mūsa River close to Ceraukste village, the Ogre Formation; exposure at the right bank of Daugava River near Lielvārde castle, exposure at the right bank of Liepna River not far from Katleši village, Kuprava quarry for mining clays, Latvia; Katleši Formation. In Russia, *B. maxima* have been found by D. Obruchev in the outcrop of sandstone, clay and sand of the Prilovat' Formation at Lovat' River close to Kurskoye Gorodische village and at the middle current of Lovat' River near Luka village. *B. maxima* was reported from the outcrops along Verkhnyaya Paluitsa and Nizhnyaya Paluitsa River surrounding Shugozero village, Tikhvin district of Leningrad region (Ivanov & Khozatski 1986). In Lithuania, *B. maxima* is found in outcrops along Nyamunelis River near Didžpanemunis and Pakalniečiai, and from borehole Stačiunai, 139.4-139.7 m deep, and borehole Petrašičnai, 57.8-58.0 m deep; Pamūšis Formation (Kratajūte-Talimaa pers. comm.). *B. maxima* is recorded also from the Jēkabpils quarry, the Katleši Formation (Sorokin 1978). *B. maxima* zone corresponds to the middle Frasnian *gigas* conodont zone. *Bothriolepis* cf. *maxima* is characteristic for the upper part of the Matusevich Formation of Severnaya Zemlya (Lukševičs 1999a).

DIAGNOSIS. — A *Bothriolepis* with the median dorsal length of the armour reaching more than 500 mm. Head-shield short and broad, B/L index about 137-156, 145 on the average, with almost flat preorbital division. Anterior margin just slightly shorter than the posterior margin, gently convex, sometimes with a rounded rostral angle. Processus obstans relatively short. Preorbital recess of trifid type. La relatively short. Nu broad and short, L/B index of about 68-75. Lateral division of the Pn relatively narrow. Trunk armour relatively low with a moderately flat dorsal wall. Dorso-lateral ridges are gently defined and rounded in their anterior part, dorsal median ridge weakly developed and practically absent in large individuals. Tergal angle situated in the foremost part of the middle third of the AMD. Ventro-lateral ridges rounded. AMD about as long as it is broad, B/L index 86-107, 97 on the average, with narrow anterior margin. PMD usually broader as it is long, B/L index about 96-117, 107 on the average; anterior margin of moderate breadth, posterior corner rounded off. Dorsal lamina of ADL about twice as long as broad, relatively narrow posteriorly the well-defined pronounced postnuchal corner; lateral lamina low. Dorsal lamina of MxL comparatively broad, from about 1.5 to 1.6 time as long as broad; lateral lamina low, about 3.5 times as long as high. Both laminae enclosing an angle about 90°. Ventral lamina of AVL about one and a half times as long as broad. MV is relatively large. Pectoral fin fairly robust, moderately long and narrow. Proximal segment about 4.5 times as long as broad; distal segment narrow, rounded in transverse section. CD5, CV5 and MM5

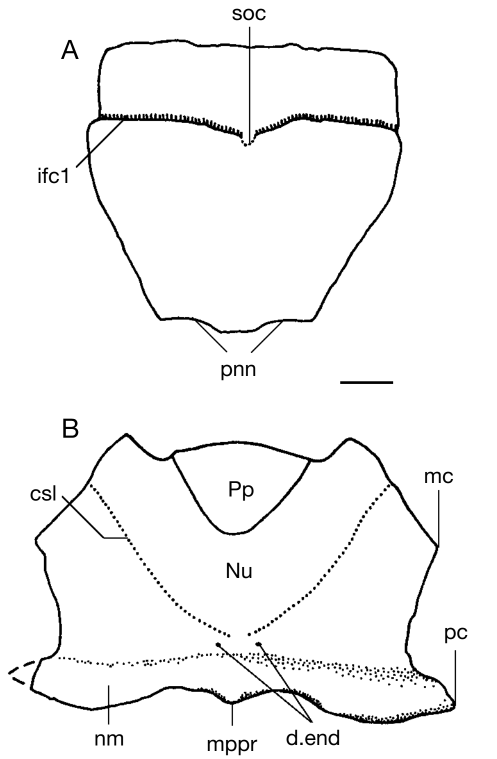

FIG. 25. — *Bothriolepis maxima* Gross, 1933; **A**, Prm PIN 2917/53 in dorsal view; **B**, Nu and Pp PIN 2917/52. Lovat' River near Luka village, Russia. Prilovat' Formation. Abbreviations: **Nu**, nuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **ifc1**, principal section of infraorbital sensory line on head-shield; **mc**, lateral corner; **mppr**, posterior process; **nm**, obtected nuchal area; **pc**, postero-lateral corner; **pnn**, nasal notch; **soc**, anterior section of the supraorbital sensory line. Scale bar: 10 mm.

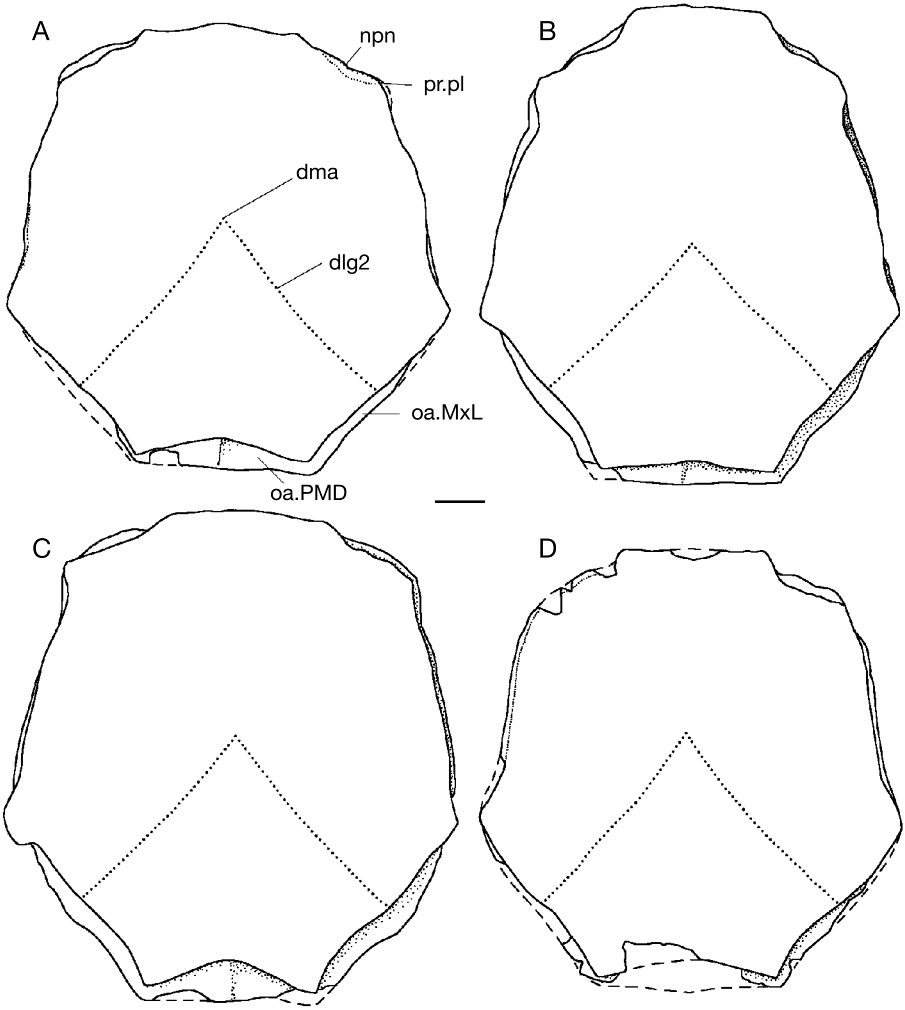

FIG. 26. — *Bothriolepis maxima* Gross, 1933, AMD; **A**, PIN 2917/42, slightly deformed; **B**, PIN 1737/63; **C**, PIN 1737/64; **D**, PIN 2917/43; **A**, **D**, Lovat' River near Luka village, Russia. Prilovat' Formation; **B**, **C**, Velna ala (Devil Cave) at the left bank of Abava River, Latvia. Ogre Formation. Abbreviations: **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **npn**, postnuchal notch; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **pr.pl**, external postlevator process of AMD. Scale bar: 20 mm.

are present. Lateral and median spines of proximal segment short and gently defined. Ornamentation reticulate, in quite large individuals retaining an on the whole reticular character, with concentrically arranged ridges; tubercular and radially arranged on the head-shield anteriorly the infraorbital sensory groove, anterior and posterior parts of the ventral wall of the trunk armour. The ornament become smooth on the pectoral fin; well-defined only in the anterior part of the CD1, CV1 and ML2.

DESCRIPTION

This is the largest known *Bothriolepis* species (Gross *in* Stensiö 1948). The largest complete AMD LDM 99/11 is 216 mm long, exceeding the largest British species, *B. gigantea*. The largest specimens with thick plates comes from Latvia, Imula and Abava River localities; the remains of the same species from the east part of the distribution area are usually smaller and less massive.

The head-shield (Fig. 23A) has the anterior margin which is only slightly shorter than the posterior margin, unlike all the other Frasnian bothriolepidoids from Baltic area. The anterior portion of the head-shield (anteriorly the orbital fenestra) is slightly elongated in comparison with that in such species as *B. obrutschewi* or *B. cellulosa*. Obstantic process is short, ending anteriorly quite well behind the transverse plane of the posterior margin of the orbital fenestra. This feature allows to distinguish *B. maxima* from *B. gigantea* which possess a long obstantic margin (Miles 1968).

The visceral surface of the head-shield (Fig. 24A) shows close resemblances with that in *B. gigantea*. The antero-lateral corner of otico-occipital depression extends forward far over the transverse plane of the anterior margin of the orbital fenestra. The paranuchal crista is straight on the La making the floor under the lateralmost part of the anterior postorbital process of endocranium, and of an irregular shape on the Pn. The transverse lateral groove is broad and shallow. The lateral pit is small, shallow and weakly defined, situated just in front of a prominent anterior crista of the transverse lateral groove, almost equally spaced from an orbital edge of the La and prelateral notch. The lateral margin shows very broad attachment areas for the Sm (Gross *in* Stensiö 1948). The orbital edges of the Prm and La are just slightly thickened, but not so thick as that in *B. ornata*.

The Prm (Figs 24C; 25A) is relatively broad, B/L index of about 99-113, 104 on the average. The La is relatively broad with the L/B index 125-134, 131 on the average. The Nu (Figs 23B; 24B; 29B) is relatively broad with the L/B index of about 68-75, 71 on the average. It is usually broadest across the posterior lateral corners or sometimes across the lateral corners, just like as in *B. gigantea* (Miles 1968). The Pn has a L/B index of about 73-83, 79 on the average, with the mesial division slightly broader than long. The lateral division of the Pn is relatively narrow (Gross *in* Stensiö 1948), composing only 44-48% of the total breadth of the plate.

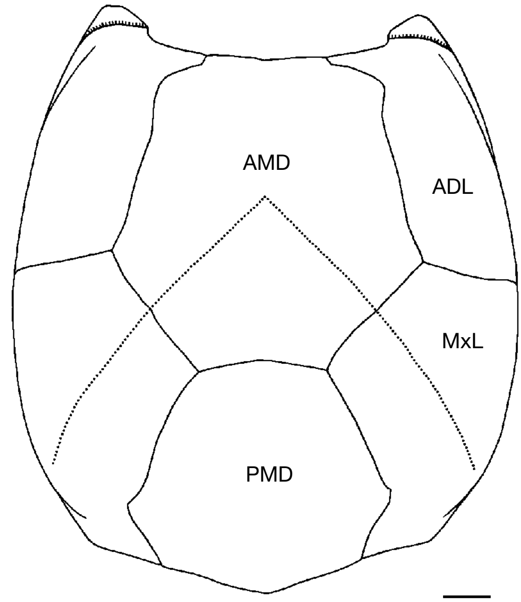

FIG. 27. — *Bothriolepis maxima* Gross, 1933, reconstruction of the trunk armour based on specimen PIN 1652/2. Right bank of Lovat' River near Luka village, Russia. Prilovat' Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate. Scale bar: 20 mm.

The complete trunk armour PIN 1652/2 (Fig. 27) is low and broad with a flat and low dorsal wall (Obrucheva 1974). Unfortunately it is almost impossible to measure correctly the angles enclosed by the dorsal and lateral wall, as well as the lateral and ventral wall due to the deformation of the trunk-armour plates during fossilization.

The AMD (Fig. 26) is about as long as it is broad with B/L index 86-107, 97 on the average. Its anterior margin is narrow, more than twice (from 2.2 to 3.3 times) as long as the plate is broad (Gross *in* Stensiö 1948) resembling *Bothriolepis ornata* in that respect. The proportions of the lateral margin of AMD vary significantly among specimens coming from different localities: the posterior division of the lateral margin is 1.3-1.9 time shorter than the anterior division in specimens from Latvia, and the same index in specimens from Luka locality in Russia reaches 1.7-2.6. Overlap areas for ADL and

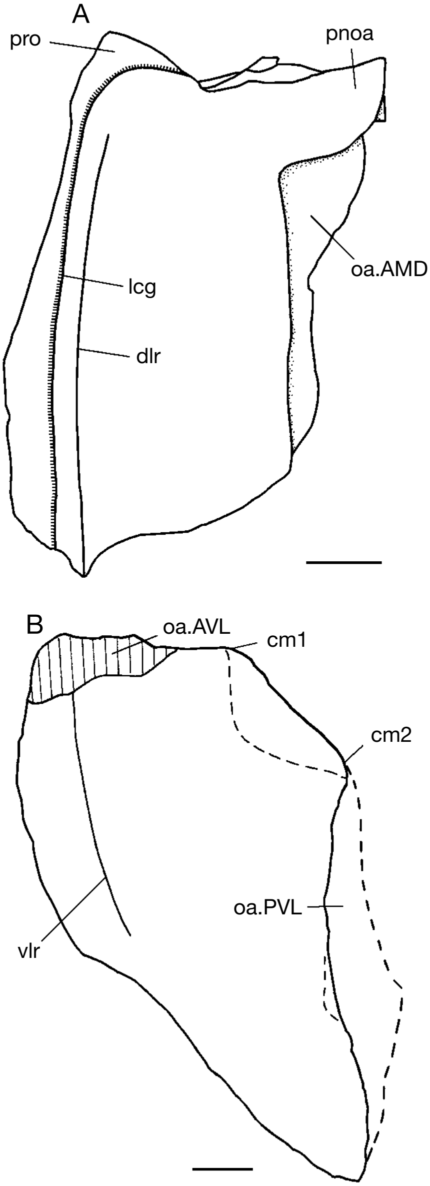

Fig. 28. — *Bothriolepis maxima* Gross, 1933; **A**, ADL PIN 1491/98, Velna ala (Devil Cave) at the left bank of Abava River, Latvia. Ogre Formation; **B**, PVL PIN 1491/88, right bank of Bolshoy Tuder River near Medovo village in vicinity of Cholm town, Russia. Prilovat' Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **PVL**, posterior ventro lateral plate; **cm1**, anteromesial corner of ventral lamina of PVL; **cm2**, middle corner of ventral lamina of PVL; **dlr**, dorso-lateral ridge of trunk armour; **lcg**, main lateral line groove; **oa.AMD**, area overlapped by AMD; **oa.AVL**, area overlapped by AVL; **oa.PVL**, area overlapped by PVL; **pnoa**, postnuchal ornamented corner; **pro**, processus obstans; **vlr**, ventro-lateral ridge. Scale bars: 20 mm.

MxL are normally developed as usually in *Bothriolepis* in general (Gross *in* Stensiö 1948), but in one case (LDM 99/11) the sutural connection of AMD with MxL is of *Remigolepis* type on the right side of the plate: the AMD overlaps the anterior part of the right MxL.

The anterior margin of PMD is of moderate breadth, 1.7-2.1 times as long as the plate totally broad. The ADL is not simply overlapped by the AVL, but also at the same time overlaps that plate posteriorly the processus obstans, as in *Bothriolepis ornata* and *B. groenlandica*. The PVL (Fig. 28B) is relatively broad, the ventral lamina is from 1.8 to 2.2 times as long as it is broad. The subanal division occupies about 30% of the total PVL length.

Remarks

Latvian material encounted here have been collected by Gross, Lyarskaja and the author from type locality and other site close to the type area. Russian material from Lovat' River is collected and illustrated by Obruchev (1947) and Obrucheva (1974), but has never been described in details.

Discussion

As the largest species of the genus, *Bothriolepis maxima* differs well from all the other representatives of the group from Baltic area first of all in its great size and very thick bones. Smallest specimens of *B. maxima* are much bigger than *B. evaldi* (for the comparison of both species see the description of *B. evaldi*), and they differ considerably from the other Baltic species in the proportions of the AMD, PMD, MxL and AVL. All the early and middle Frasnian *Bothriolepis* in this area could be well-recognized by their preorbital recess of a simple type, and only *B. maxima* among them possess the preorbital recess of a trifid type. *B. maxima* resembles *Bothriolepis gigantea* (Stensiö 1948; Miles 1968) from Scotland in several aspects and these species seems to be very closely related phylogenetically. Nevertheless, as it was pointed out by Gross (*in* Stensiö 1948), Stensiö (1948) and Miles (1968), there are several features distinguishing these two species. Adding the list of such a features provided by Miles, it is possible to suggest that *B. maxima* differs from *B. gigantea* in its 1) shorter obstantic margin; 2) presence of the lateral pit on the visceral surface of the La; 3) well-defined nasal notches on the Prm; 4) other shape of the posterior margin of the head-shield; 5) structure of the transverse nuchal crista; 6) more sharp angle between the dorsal and lateral laminae of the MxL.

Bothriolepis evaldi Lyarskaja, 1986 (Figs 29-31)

Bothriolepis evaldi Lyarskaja, 1986: 123-130; pl. I, fig. 1.

HOLOTYPE. — Articulated head-shield, trunk-armour and pectoral appendages LDM 67/86.

MATERIAL EXAMINED. — LDM 67/2-4, 67/6-77, 67/79, 67/80, 67/89-93: 62 articulated head-shields, trunk-armour and pectoral appendages, as well as 18 disarticulated plates of the armour from the type locality; LDM 280/1: head-shield, 280/2-27: mostly disarticulated plates of the trunk armour and pectoral fin from the Kaibala River site.

LOCALITIES AND HORIZON. — The type locality Kalnamuiža-1 (number 5 in Fig. 1) is cliff at the left bank of Amula River downstream from water-mill Kalnamuiža with grey sandstone and thin layers of blue marls; the Middle Frasnian, the Rembate Member of the Ogre Formation (Lyarskaja 1986). Other material comes from an outcrop exposing similar deposits at the right bank of Kaibala River (number 12 in Fig. 1) 200 m from the estuary, not far from ruins of Lielvārde castle.

DIAGNOSIS. — Small *Bothriolepis* with a median dorsal armour length reaching about 50 mm. B/L index of trunk armour about 95. B/L index of the head-shield 140-157. Rostral margin of the head-shield strongly convex. Orbital fenestra relatively small, broad, slightly less than twice as broad as it is long. Nu arched, moderately broad, L/B index of 69. Trunk-armour of moderate height with broad and high dorsal wall. Dorsal and lateral walls of trunk enclosing an angle about 126° on MxL. Dorso-lateral and ventro-lateral ridges well-marked. Median dorsal ridge well-defined posteriorly the tergal angle. Ventral wall of the trunk-armour relatively narrow, B/L index 43-48. AMD broad, B/L index 84-108, arched, with right and left laminae forming an angle of about 128°. Anterior margin broad, almost straight. Postlevator cristae on the visceral surface of AMD are well-defined. AMD overlaps the MxL by the anterior part of the posterior division of lateral margin in medium-sized individuals. PMD moderately broad with pronounced posterior corner. Dorsal lamina of MxL about 1.6-2.2 times as broad as the lateral lamina is high. The dorso-ventral pit-line groove on the MxL is usually present. Proximal segment of the pectoral appendage moderately long, about 3.6 times as longs as it is broad and less then twice longer than the distal segment. Ornamentation fine reticulate, becoming slightly coarser and sparser in medium-sized individuals.

DESCRIPTION

This species is well-represented at the type locality by many articulated head-shields, trunk-armours and pectoral appendages, as well as some disarticulated plates. Most specimens from this locality are slightly flattened, often deformed. Size range is from a median dorsal trunk-armour (LDM 67/10, Fig. 29G) less than 17 mm long to an individual with a median dorsal armour length estimated of about 34 mm. Material from the Kaibala site is represented by larger plates, an articulated head-shield LDM 280/1 (Fig. 30D) suggests a median dorsal armour length estimated of about 48 mm. The head-shield is well-preserved in 22 specimens. It is relatively broad in small individuals, Lyarskaja (1986) mentions B/L index varying from 118 to 170, but my measurements and estimations show the B/L is 140-157, 145 on the average (n = 8), and reaching only 120 in medium-sized individual. The head-shield is strongly vaulted both rostrocaudally and transversely (Lyarskaja 1986). The rostral margin is convex, shorter than the posterior margin; the anterolateral corners and a shallow prelateral notch are clearly defined only in individuals of medium size (Lyarskaja 1986). The obtected nuchal area is short, broadest on the Nu. The orbital fenestra is relatively small, but very broad with a B/L index about 168-196, 185 on the average. A new material (LDM 280/1) allows to identify the shape of the preorbital recess, which is of simple type.

The visceral skull surface shows the normal features as a prominent transverse nuchal crista, well-developed median occipital crista, and a very broad otico-occipital depression which is

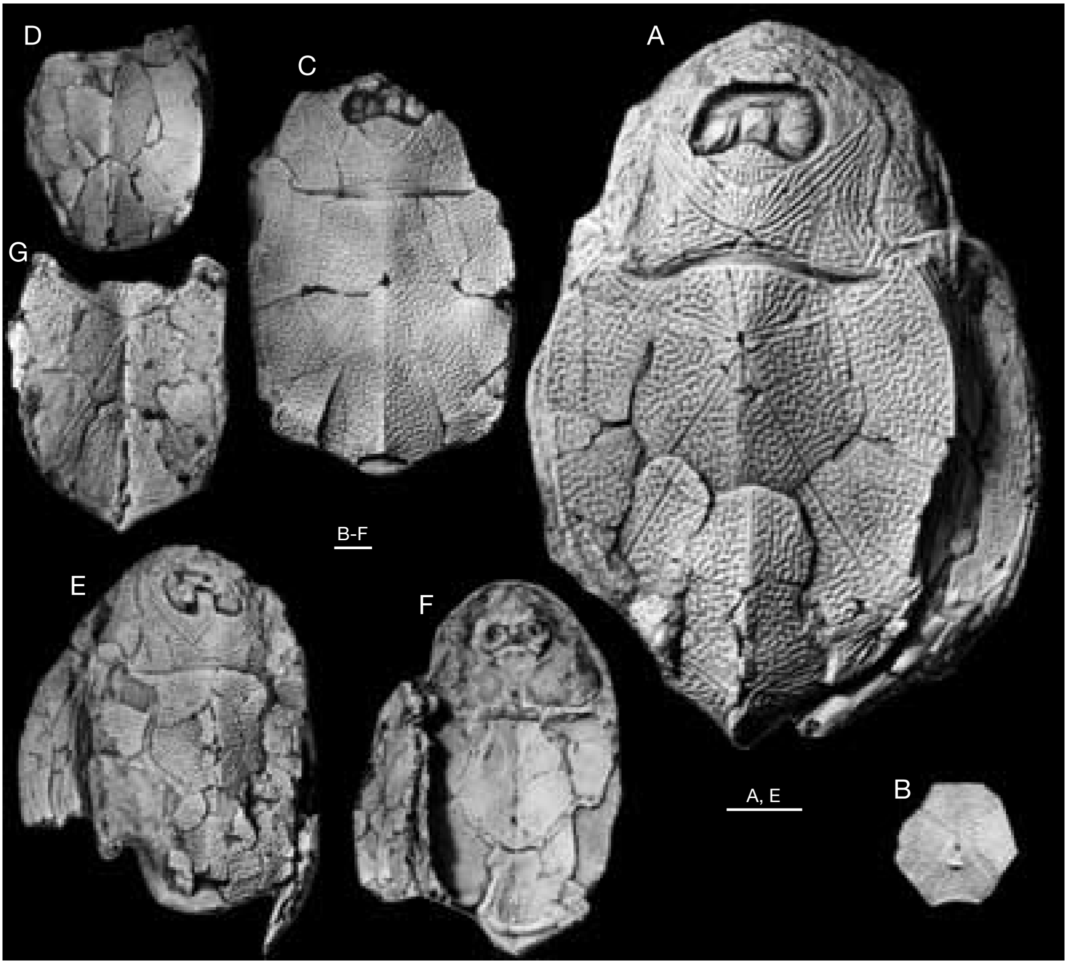

FIG. 29. — *Bothriolepis evaldi* Lyarskaja, 1986; **A**, holotype, articulated head, trunk and pectoral fin armour LDM 67/86 in dorsal view; **B**, AMD LDM 67/7; **C**, articulated head and trunk armour LDM 67/14 in dorsal view; **D**, articulated trunk armour LDM 67/2 in dorsal view; **E**, articulated head, trunk and pectoral fin armour LDM 67/39; **F**, head and trunk armour in visceral view with articulated right pectoral fin in ventral view LDM 67/6; **G**, articulated trunk armour LDM 67/10 in dorsal view. Kalnamuiža 1 locality at Amula River, Latvia. Ogre Formation. Abbreviation: **AMD**, anterior median dorsal plate. Scale bars: 5 mm.

well-defined by the paramarginal cristae. The median ridge sharing the broad paired pits of Pp is low.

The Prm was not described by Lyarskaja (1986). It is broad, much broader than it is long in small specimens with B/L index 150-182, which decreases to 103 in largest individuals. The Prm is broadest at the infraorbital sensory groove or rostral margin. The rostral margin is convex, it is 1.2-1.4 time longer then the almost straight orbital margin. The nasal notch on the orbital margin can be recognized only slightly in medium-sized specimen LDM 280/1. There is a median elevation inside the rostral margin. The infraorbital sensory groove crosses the plate in its anterior part.

The La is moderately broad with the L/B index 126-143, 134 on the average. The infraorbital sensory groove crosses the plate in its anterior part not far from the orbital and lateral margins (Lyarskaja 1986). The central sensory line groove (csl) usually is finished at the level of the

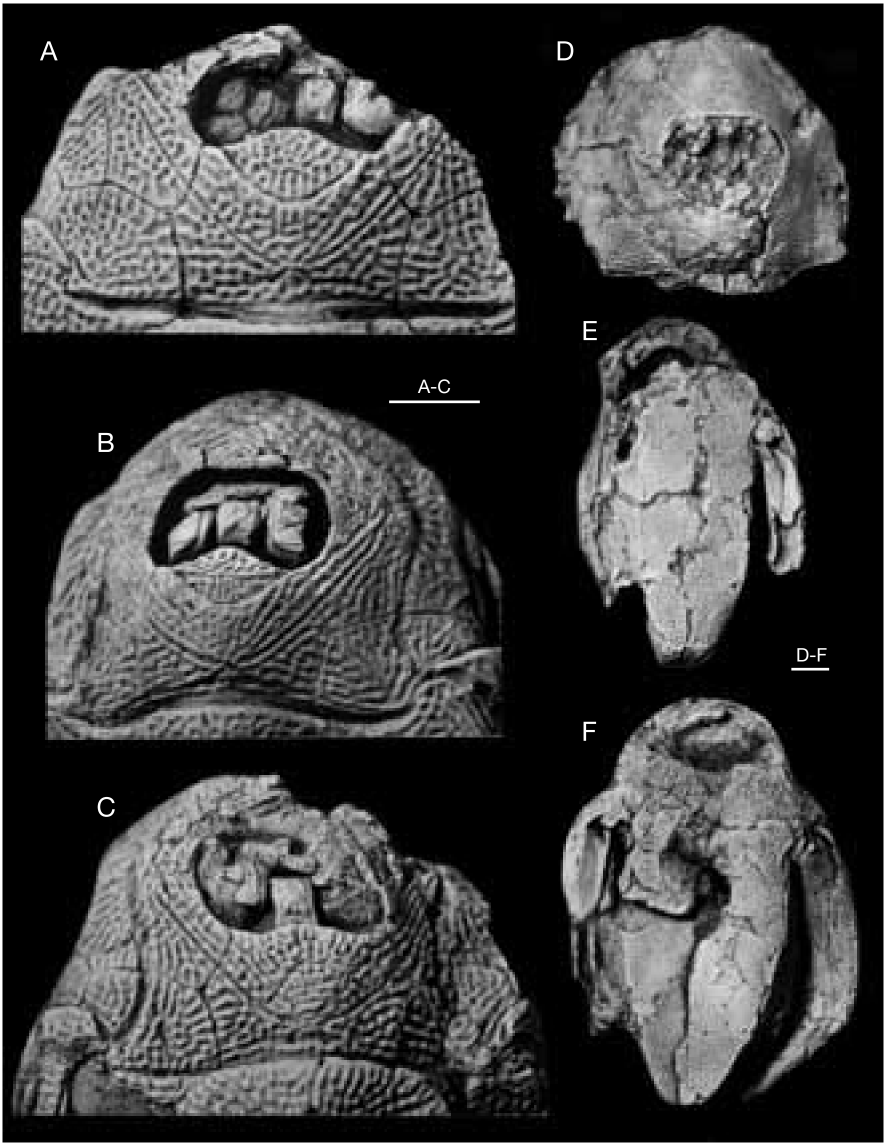

FIG. 30. — *Bothriolepis evaldi* Lyarskaja, 1986; **A**, details of the head-shield of specimen LDM 67/14 in dorsal view; **B**, details of the head-shield of the holotype, LDM 67/86; **C**, details of the head-shield of specimen LDM 67/39 in dorsal view; **D**, head-shield LDM 280/1 in dorsal view; **E**, somewhat flattened and deformed articulated head, trunk and left pectoral fin armour LDM 67/13 in ventral view; **F**, articulated head, trunk, left pectoral fin armour and right CV1 LDM 67/3 in ventral view; **A**-**C**, **E**, **F**, Kalnamuiža 1 locality at Amula River, Latvia; **D**, Kaibala River not far from Lielvārde, Latvia. Ogre Formation. Abbreviation: **CV1**, ventral central plate 1. Scale bars: 5 mm.

middle of the orbital fenestra length, sometimes it extends almost to the anterior margin of the orbital fenestra (Lyarskaja 1986). The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc2) are well-defined (Lyarskaja 1986).

The pineal plate is moderately narrow, slightly longer than it is broad, and not quadrate, as has

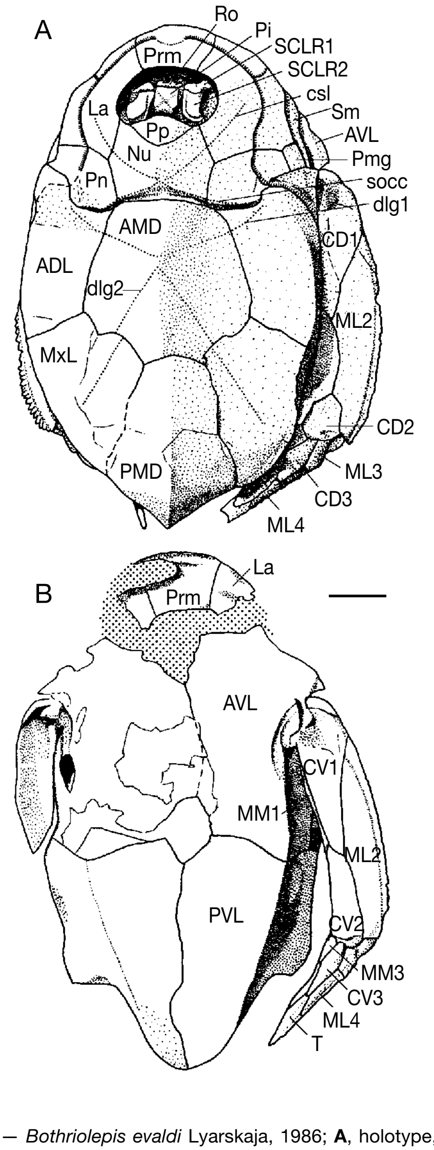

FIG. 31.— *Bothriolepis evaldi* Lyarskaja, 1986; **A**, holotype, the articulated head-shield, trunk armour and pectoral fins LDM 67/86 in dorsal view; **B**, articulated head-shield, trunk armour, left pectoral fin and CD1 LDM 67/3 in ventral view, with dotted space showing the matrix. Kalnamuiža 1 locality at Amula River, Latvia. Ogre Formation. Abbreviations: **ADL**, anterior dorsolateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD1-3**, dorsal central plates 1-3; **CV1-3**, ventral central plates 1-3; **La**, lateral plate; **ML2-4**, lateral marginal plates 2-4; **MM1**, **3**, mesial marginal plates 1, 3; **MxL**, mixilateral plate; **Nu**, nuchal plate; **Pi**, pineal plate; **PMD**, posterior median dorsal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **PVL**, posterior ventro lateral plate; **Ro**, rostral plate; **SCLR1**, **2**, plates 1 and 2 of sclerotic ring; **Sm**, submarginal plate; **T**, terminal plate; **csl**, central sensoty line; **dlg1**, **2**, anterior and posterior oblique dorsal sensory line grooves; **socc**, supraoccipital cross-commissural pit-line groove. Scale bar: 5 mm.

been shown by Lyarskaja (1986). The all four margins of the plate are concave. Position of the pineal pit is marked on the outer surface by the pineal elevation (Lyarskaja 1986).

The Pp is broad in small individuals and of moderate breadth in maturity, L/B index varies from 44 to 55. Lyarskaja (1986) claimed that the shape of the plate is almost constant, but in fact the anterior margin is strongly convex in small specimens and became more straight with increasing size, as in other species of *Bothriolepis*.

The Nu has L/B index 64-76, 69 on the average. The plate is broadest across the lateral corners (Lyarskaja 1986). The anterior division of the lateral margin usually is concave and a little shorter than the posterior division. The posterior margin usually is almost straight, the posterior process is weakly defined. The central sensory line groove is clearly distinct (Lyarskaja 1986). In some cases there are long supraoccipital grooves (socc), which cross the plate little in front of the obtected nuchal area and extend to the Pn. The external openings for the endolymphatic ducts (d.end) are rather large, closely set one to another. Postorbital crista on the visceral surface is low, clearly seen only in largest individuals (Lyarskaja 1986). Specimen LDM 67/39 shows very unusual feature, which have not been mentioned by Lyarskaja (1986): the Nu is fused with the Pp (Fig. 30C).

The Pn is broad, L/B index 70-83, 76 on the average. The lateral division of the Pn is relatively broad and is composing 33-52% of the general breadth of a plate. The middle pit-line groove (mp) always present.

The Pmg is broad with the lateral margins longer than the median margins (Lyarskaja 1986).

The sclerotic ring is preserved in some specimens. Its features seem to be similar to that of the ring of *Bothriolepis canadensis* (see Stensiö 1948) or *B. hydrophila* (see Miles 1968).

The Sm (extralateral) plate is always badly preserved. It seems to be relatively long and narrow (Lyarskaja 1986).

The trunk-armour is broad (Lyarskaja 1986), B/L index 87-99, 95 on the average (n = 10). It is relatively high, with a lateral wall 2.5 times as long as high; the dorsal wall is moderately arched with well-defined median dorsal ridge. Length of the dorsal wall, probably, reaches about 50 mm. The shape and proportions of the ventral wall are similar to that of *Bothriolepis prima* (see Lyarskaja 1986); B/L index 43-48.

Anterior margin of the AMD is 1.1-1.6 time as long as the posterior margin. The antero-lateral corner, postnuchal notch (npn) and the postlevator processes (pr.pl) are well-defined, as are the obtuse lateral and postero-lateral corners (Lyarskaja 1986). The posterior division of the lateral margin is 1.6-2.5 (2.2 on the average) times shorter than the anterior division. The tergal angle (dma) is situated in between the anterior third and middle of the plate and is well-marked, the median dorsal ridge (dmr) is strongly developed (Lyarskaja 1986). Overlap areas for ADL and MxL are developed as usually in *Bothriolepis* in small individuals, but in specimens of medium size the overlap area for MxL is developed as in *Remigolepis* (Lyarskaja 1986). The anterior oblique dorsal sensory line grooves (dlg1) are well-defined on the plates of small individuals. The posterior oblique dorsal sensory line grooves (dlg2) are also well-defined (Lyarskaja 1986).

The PMD is arched, moderately broad, B/L index 88-105, 95 on the average. The width of the anterior margin comprises 44-55% of total breadth (50% on the average). The median dorsal ridge is strongly developed (Lyarskaja 1986).

The ADL is slightly longer than the MxL in articulated armour. The dorsal lamina is moderately broad, its breadth exceeds height of the lateral lamina. The dorso-lateral ridge (dlr) is well-defined (Lyarskaja 1986). The postnuchal ornamented corner (pnoa) is sharp, long and narrow.

The dorsal lamina of the MxL is moderately broad, 1.4-1.6 time as long as it is broad. The dorsal lamina is 1.6-2.2 times as broad as the lateral lamina is high. Dorsal and lateral laminae enclosing an angle about 126°. The lateral lamina is moderately high, 2.4-3.2 times as long as it is broad. The dorso-lateral ridge is well-defined (Lyarskaja 1986). The overlap area for the AMD is restricted to half the length of the antero-dorsal margin as in *Remigolepis* (Stensiö, 1931). The posterior oblique sensory line groove (dlg2) in some cases terminates in some distance from the lateral margin, but usually the dorso-ventral pit-line groove (dxp) crossing the dorso-lateral ridge is present (Lyarskaja 1986).

The AVL is broad, the ventral lamina is 1.4-1.7 time as long as it is broad. The subcephalic division 26-33% of total length of the ventral lamina. The ventral lamina 2.2 times as broad as the lateral lamina high in LDM 67/13 (Fig. 30E). The lateral lamina is moderately high, about twice as long as it is high. Ventro-lateral ridge is well-defined. The axillary foramen is rather large and slightly elongated in shape (Lyarskaja 1986).

The PVL has similar proportions to the AVL, as in most *Bothriolepis* species. It is of moderate breadth, the ventral lamina is 2-2.3 times as long as it is broad. The subanal division is relatively narrow (Lyarskaja 1986) and occupies 20-27% of the total PVL length. The lateral lamina is relatively high, 1.9-2.2 times as long as it is high. The ventral lamina is 1.3-1.5 time as broad as the lateral lamina high. The ventro-lateral ridge is well-developed.

The length/ breadth index of the MV is 1.1 in LDM 67/54.

The pectoral fin is represented mostly by articulated bones. The proximal segment is about 1.9 time longer than the distal segment. Both segments bear small lateral and mesial spines in small individuals. Individuals of medium size have the proximal segments bearing prominent lateral spines, which are fused in their base forming well-defined crest. The proximal segment is of moderate breadth, 3.3-4 (3.6 on the average) times as long as it is broad. The CD1 is with L/B index varying from 2.7 to 3.3, 3 on the average. The CV1 is slightly longer than the CD1 and have similar proportions. The ML2 is 4.2-4.6 (4.4 on the average) as long as it is broad. The distal segment shows CD3 and CD4, it is long and relatively narrow.

The ornamentation is typically reticulate, becoming slightly coarser and sparser in medium-sized individuals. The network of anastomosing ridges are broken into shorter ridges along the margins of the plates. The ornamentation of the pectoral appendage is reticulate in general, on the CD1 the ornament is radially arranged, on the distal segment it consists of longitudinal gently defined ridges. The T has almost smooth surface.

REMARKS

The following account is the first full treatment in English, which supplements Lyarskaja's description (in Russian) of *Bothriolepis evaldi* (1986), adding some details. It is based on specimens from Lyarskaja's collection from the type locality, kept at the Latvian Museum of Natural History, and material from the Kaibala site, gathered by the author.

DISCUSSION

Most part of materials on *Bothriolepis evaldi* from the type locality shows the following features, which can be considered to indicate immature individuals: 1) the proportionally large orbital fenestra; 2) the breadth of the Prm; 3) the shape of the Pp with strongly convex anterior margin; 4) the relatively broad lateral division of the Pn; 5) the poor development of the median ventral ridge on the visceral surface of the AMD; 6) the strong development of the dorsal median ridge; 7) the presence of the anterior oblique dorsal sensory line groove and dorso-ventral pit-line groove. However the largest specimens from the Kaibala locality seem to be from well-grown individuals. *B. evaldi* resembles *B. maxima* by many features: 1) broad Nu; 2) shape and proportions of the AMD and ADL; 3) shape of the postnuchal ornamented corner of the ADL; 4) situation of the tergal angle, etc. Nevertheless, *B. evaldi* differs from *B. maxima* in its 1) much smaller size; 2) shape of the preorbital recess; 3) shape and proportions of the PMD; 4) strongly developed dorsal median, dorso-lateral and ventro-lateral ridges. The largest AMD from the Kaibala locality LDM 280/8 which is about 50 mm long and seem to be from well-grown individual, retain the strongly developed dorsal median ridge. Smallest AMD of *B. maxima* PIN 89/4 is 104 mm long and shows only gently defined dmr. The largest (33.3 mm long) head-shield of *B. evaldi* LDM 280/1 possess the preorbital recess of simpe type, but smallest (97 mm long) head-shield of *B. maxima* LDM 84/67 has trifid preorbital recess. Specimens from Kaibala site are important because they lead to evaluate two hypothese: 1) *B. evaldi* does not comprise juveniles of the larger, contemporaneous species *B. maxima*, which occurs with *B. evaldi* in the Ogre Formation; or 2) shape of the preorbital recess changes dramatically during ontogeny. Resemblances and differences between these two species as they have been described by Lyarskaja (1986) could be explained mostly by allometric pattern of growth.

B. evaldi can be distinguished readily from *B. obrutschewi* (Karatajūte-Talimaa 1966), *B. cellulosa* (Gross 1942) and *B. panderi*, other Frasnian *Bothriolepis* representatives from the Main Devonian field.

B. evaldi resembles *B. prima* from the Main Devonian field and *B. hydrophila* (Miles 1968) from Scotland by several features. *B. evaldi* differs from *B. prima* in its 1) relatively smaller orbital fenestra; 2) shape of the Prm; 3) strongly developed median dorsal ridge; 4) shape of the postlevator cristae on the visceral surface of the AMD. *B. evaldi* differs from *B. hydrophila* in its 1) smaller size; 2) much broader dorsal wall of the trunk-shield; 3) shape and proportions of the AMD; 4) shape of the postnuchal ornamented corner of the ADL; 5) narrower ventral wall of the trunk-shield; 6) shorter proximal segment of the pectoral fin.

Bothriolepis leptocheira Traquair, 1893
(Figs 32-39)

Pterichthys major – Geikie 1869: 12-13 (after Miles 1968).

Bothriolepis major Ag. – Traquair 1888: 510 (after Miles 1968).

Bothriolepis leptocheirus Traquair, 1893: 285-286. — Stensiö 1931: 164.

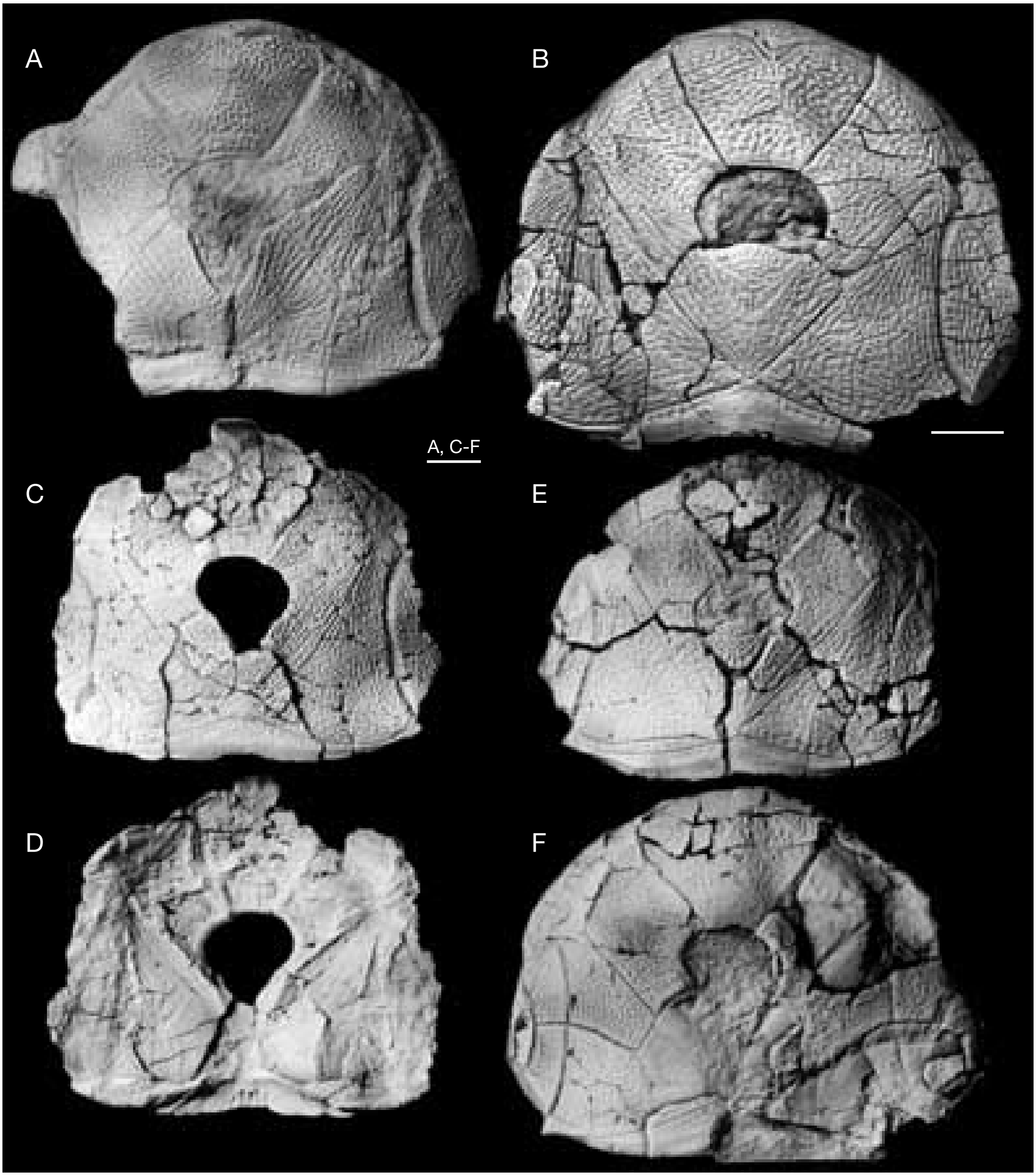

FIG. 32. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, head-shield LDM 15/32; **B**, head-shield LDM 98/12; **C**, **D**, head-shield LDM 98/108 in dorsal and visceral views; **E**, head-shield LDM 98/86; **F**, head-shield LDM 89/1; **A**, Imula River near Bienes hamlet, Latvia; **B**-**F**, Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Scale bars: 10 mm.

Bothriolepis leptocheira Traquair – Evans *in* Miles 1968: 112.

Bothriolepis curonica Gross, 1942: 420, 421, abb. 10. — Stensiö 1948: 615. — Lukševičs 1987: 90, text-figs 1-6.

For a full list of synonyms before 1965 see Miles (1968).

TYPE SPECIMEN. — Gross (1932: 26) selected the AVL plate RSM 1859.33.19A as a lectotype illustrated by Traquair (1906: pl. 29, fig. 3).

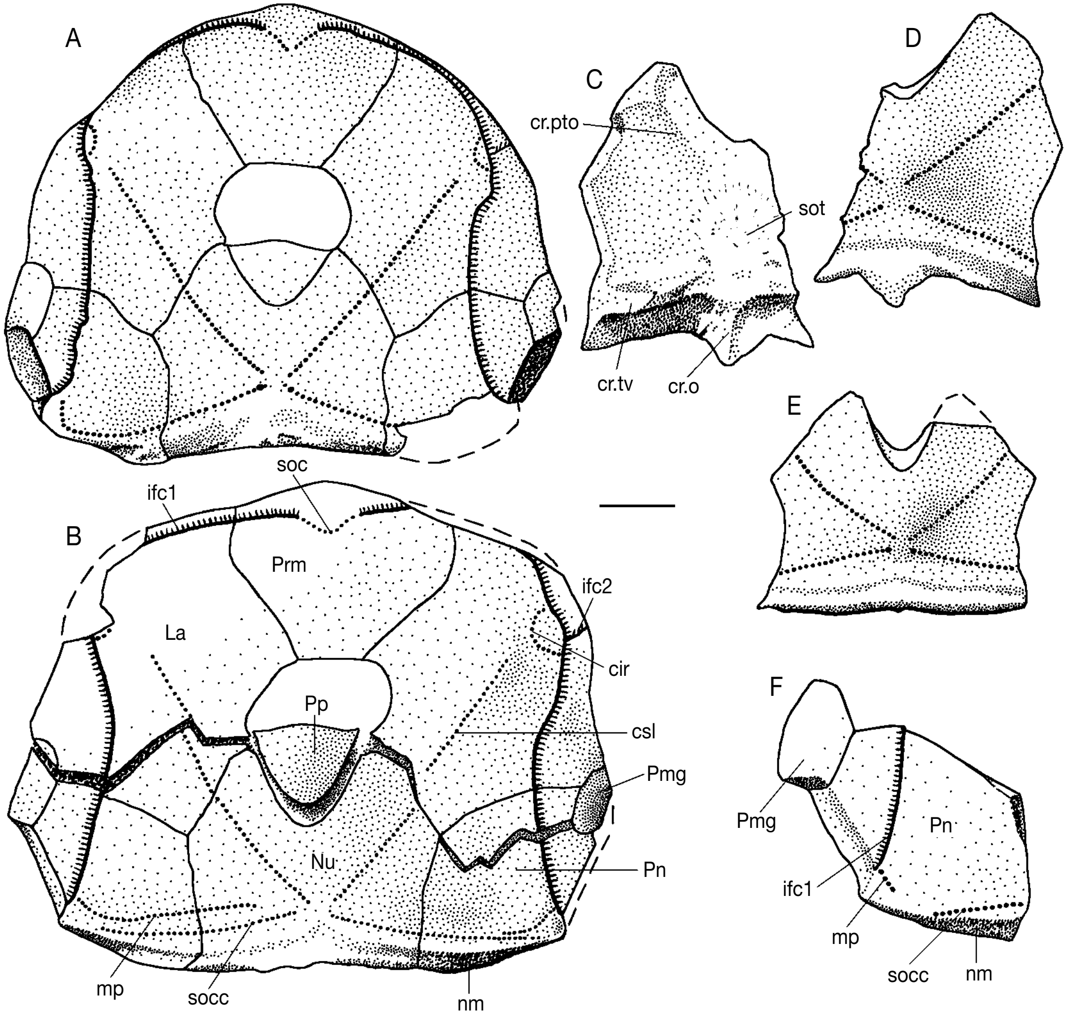

FIG. 33. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, **B**, head-shields in dorsal view; **A**, LDM 98/12; **B**, LDM 98/86; **C**-**E**, Nu; **C**, **D**, LDM 98/20 in visceral and dorsal views; **E**, LDM 98/13 in dorsal view; **F**, articulated Pn and Pmg LDM 98/18 in dorsal view. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **cir**, semicircular pit-line groove; **cr.o**, median occipital crista; **cr.pto**, postorbital crista; **cr.tv**, transverse nuchal crista; **csl**, central sensory line groove; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **mp**, middle pit-line groove; **nm**, obtected nuchal area; **soc**, anterior section of the supraorbital sensory line; **socc**, supraoccipital cross-commissural pit-line groove; **sot**, supraotic thickening. Scale bar: 10 mm.

MATERIAL EXAMINED. — Apart from the British material (Miles 1968), LDM 15/33 (AMD, PMD), 15/34, 15/121, 65/110-118, 121, 123, 130, 133, 89/1-15, 89/27, 89/28, 98/1-68, 98/76-89, 98/91,98/94-101: articulated head-shields and pectoral appendages, disarticulated plates of the trunk-armour and pectoral fin. All these specimens come from Latvia.

LOCALITIES AND HORIZON. — The type locality is Bracken Bay, Ayrshire (Heads of Ayr), Scotland; the Upper Old Red Sandstone. In western Latvia, it has been collected in the right bank of Imula River near Bienes hamlet (number 3 in Fig. 1); stratotype of the Amula Formation and exposure of dolomite marls, clays and siltstones of the Eleja Formation at the right bank of Amula River 1 km upsteam from water-mill Kalnamuiža (number 6 in Fig. 1); the Purviņi Member of the Eleja Formation, lowermost upper Famennian. A possible new subspecies of *B. leptocheira* occurs in the Malyutka Formation of Severnaya Zemlya, outcrops along Matusevich River (Lukševičs 1999a).

DIAGNOSIS. — Rather large *Bothriolepis* with a median dorsal armour length of at least 240 mm. B/L index of dorsal wall of trunk-armour about 77. B/L index of the head-shield of 130. Preorbital recess of trifid type. Anterior margin of the head-shield is rounded. Orbital fenestra is relatively small. Prm broad, orbital margin is much shorter than rostral margin. Nu L/B index of 84, with very short orbital facets. Supraoccipital groove long, sometimes fused with a long middle pit-line. AMD relatively narrow, B/L index 83, with the relatively short anterior margin. PMD broad with narrow anterior margin. Median dorsal ridge poorly developed in posterior part of PMD. Dorso-lateral and ventro-lateral ridges are well-marked. Both AVL and PVL are elongated. Proximal segment of the pectoral appendage is long and slender, 5.5 times as longs as it is broad. Ornamentation is fine and basically of reticular type, in quite large individuals becoming smooth.

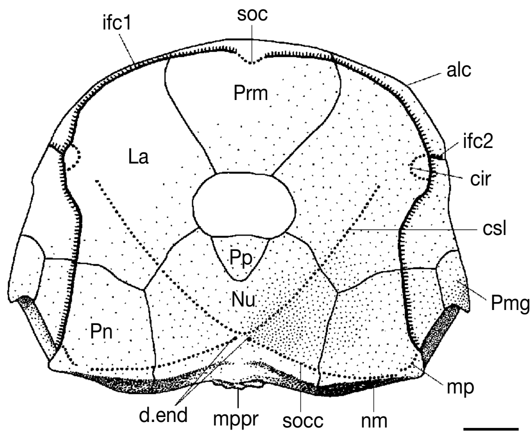

FIG. 34. — *Bothriolepis leptocheira curonica* Gross, 1942, attempted reconstruction of the head-shield, based on LDM 89/1. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **alc**, antero-lateral angle of head-shield; **cir**, semicircular pit-line groove; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **mp**, middle pit-line groove; mppr, posterior process on Nu; **nm**, obtected nuchal area; **soc**, anterior section of the supraorbital sensory line; **socc**, supraoccipital cross-commissural pit-line groove. Scale bar: 10 mm.

DESCRIPTION

This species is well-represented in clay of the Kalnamuiža locality by many articulated skulls, some articulated proximal segments of the pectoral fin, as well as disarticulated plates of the trunk-shield and pectoral appendage. Most are from individuals of moderate size. The plates are usually flattened, often deformed. The head-shield is moderately broad, with average B/L index 130 (n = 10), slightly narrower than the head-shield (B/L index 142) restored by Miles (1968); the differences in breadth could be explained by difficulties in restoration of a correct shape and proportions of the head-shield from disarticulated plates. As in Scottish material, the rostral margin is convex, rounded, usually slightly longer than the posterior margin. The head-shield is weakly vaulted both rostrocaudally and transversely, as in Scottish material, but the anterior part of the Prm and La is strongly curved. The antero-lateral corner (alc), the prelateral notch and the lateral process are weakly defined, not seen in dorsal view. The orbital fenestra is relatively small, with a B/L index varying from 175 in individuals of moderate size to 150 in largest individuals. The preorbital recess both in Latvian and Scottish material (Miles 1968: text-fig. 36) is of trifid type, but with the lateral horns less extended laterally than that in *B. maxima* or *B. gigantea*, and more broad at their base. The orbital edges of the Prm and La are not thickened (this feature is not seen in Scottish material). The antero-lateral corners of otico-occipital depression on the visceral surface of the head-shield extend forward so that they end just in front of the transverse plane of the anterior margin of the orbital fenestra, as in Scottish material (Miles 1968: 76).

The Prm is weakly arched, with B/L index 123-148, broader than Prm in Scottish material (Miles [1968] has mentioned B/L index of 114, 120 and 128). The rostral margin is convex, it is three times longer than the slightly concave orbital margin in material from both countries (for comparison see Figs 32-34 and Miles 1968: pl. 20, figs 1, 2). Also such characters as the position of the infraorbital sensory groove (ifc1) which crosses the plate close to its rostral margin, and a well-defined anterior section of the supraorbital sensory line (soc), are similar.

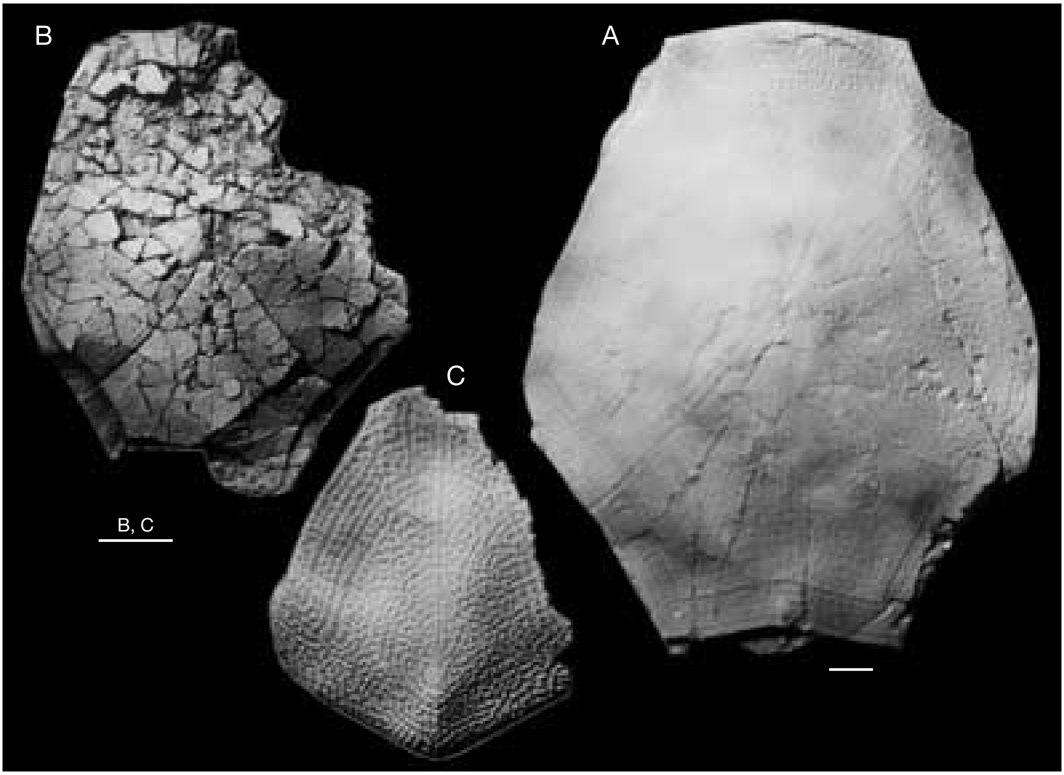

FIG. 35. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, AMD LDM 15/121, Imula River near Bienes hamlet, Latvia. Eleja Formation; **B**, AMD LDM 98/21; **C**, PMD LDM 98/36. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **AMD**, anterior median dorsal plate; **PMD**, posterior median dorsal plate. Scale bars: 10 mm.

The La "is of the short, broad type" (Miles 1968: 77). The L/B index of the La of 120-128, 124 on the average in Latvian material. The Pp has L/B index varying from 69 to 83, it is elongated in both material from Scotland (Miles 1968: pl. 20, fig. 4) and Latvia, e.g., LDM 89/1 (Fig. 34).

The Nu has the L/B index about 84 (Miles mentions L/B index 83). The plate is always broadest across the lateral corners. The anterior division of the lateral margin is usually convex (RSM 1859.33.632A and B, LDM 98/12, 13, 20, 86, Fig. 33, etc.), and a little shorter than the posterior division.

The Pn is of moderate breadth, L/B index about 86, Miles (1968) has restored it with L/B index of about 80. The lateral division of the Pn is relatively narrower than in *B. ciecere* and is composing 34-45% (38.7 on the average) of the general breadth of a plate. Long supraoccipital groove (socc) usually is present in Latvian material, it terminates usually at the level of the middle of the plate posterior margin. The middle pit-line groove (mp) is always present, sometimes it is very long (LDM 98/86, Fig. 33B) or (LDM 98/3, 7, 12, 89/5, Fig. 33A) it fuses with the supraoccipital groove. This character was not described or drawn by Miles (1968: text-fig. 36) and not clearly seen in his illustrations; however RSM 1859.33.632B shows long supraoccipital groove and the middle pit-line groove also on the Pn (pers. obs.).

The trunk-armour is narrow, relatively low, with rather flattened low dorsal wall and the lateral wall more than three times as long as high. Length of the dorsal wall, probably, is more than 240 mm (Miles [1968] estimated the dorsal

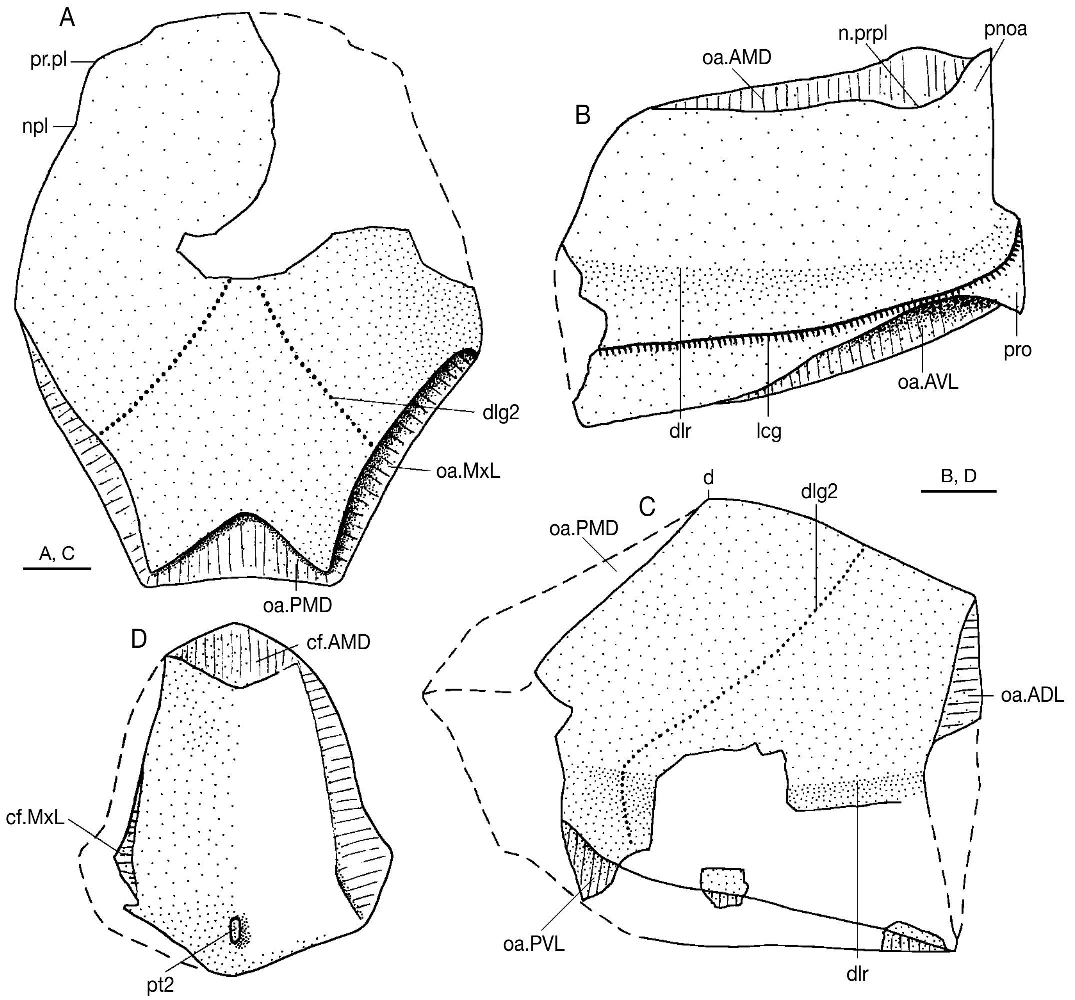

FIG. 36. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, AMD LDM 98/21 in dorsal view; **B**, ADL LDM 98/58; **C**, MxL LDM 98/53; **D**, PMD LDM 98/35 in visceral view. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **cf.AMD**, area overlapping AMD; **cf.MxL**, area overlapping MxL; **d**, dorsal corner; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge; **dmr**, dorsal median ridge; **l**, lateral corner; **lcg**, main lateral line groove; **npl**, postlevator notch; **n.prpl**, notch in dorsal margin of ADL for external postlevator process of AMD; **oa.ADL**, area overlapped by ADL; **oa.AMD**, area overlapped by AMD; **oa.AVL**, area overlapped by AVL; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **oa.PVL**, area overlapped by PVL; **plc**, postero-lateral corner; **pnoa**, postnuchal ornamented corner; **pro**, processus obstans of trunk armour; **pr.pl**, external postlevator process; **pt2**, posterior ventral pit. Scale bars: 10 mm.

wall reached a length of some 140 mm). The ventral wall is narrow, with B/L index about 53 in Latvian material. The subcephalic and subanal divisions are relatively long.

The AMD is weakly arched, narrow, B/L index about 83 in Latvian material, and about 77 in Scottish material (Miles 1968: 78). The antero-lateral and lateral corners, and the postlevator processes (pr.pl) are well-defined (Miles 1968: text-fig. 37; Fig. 35A). The posterior division of the lateral margin is 1.4-1.6 time shorter than the anterior division. There is no median dorsal ridge neither in Scottish, nor in Latvian material.

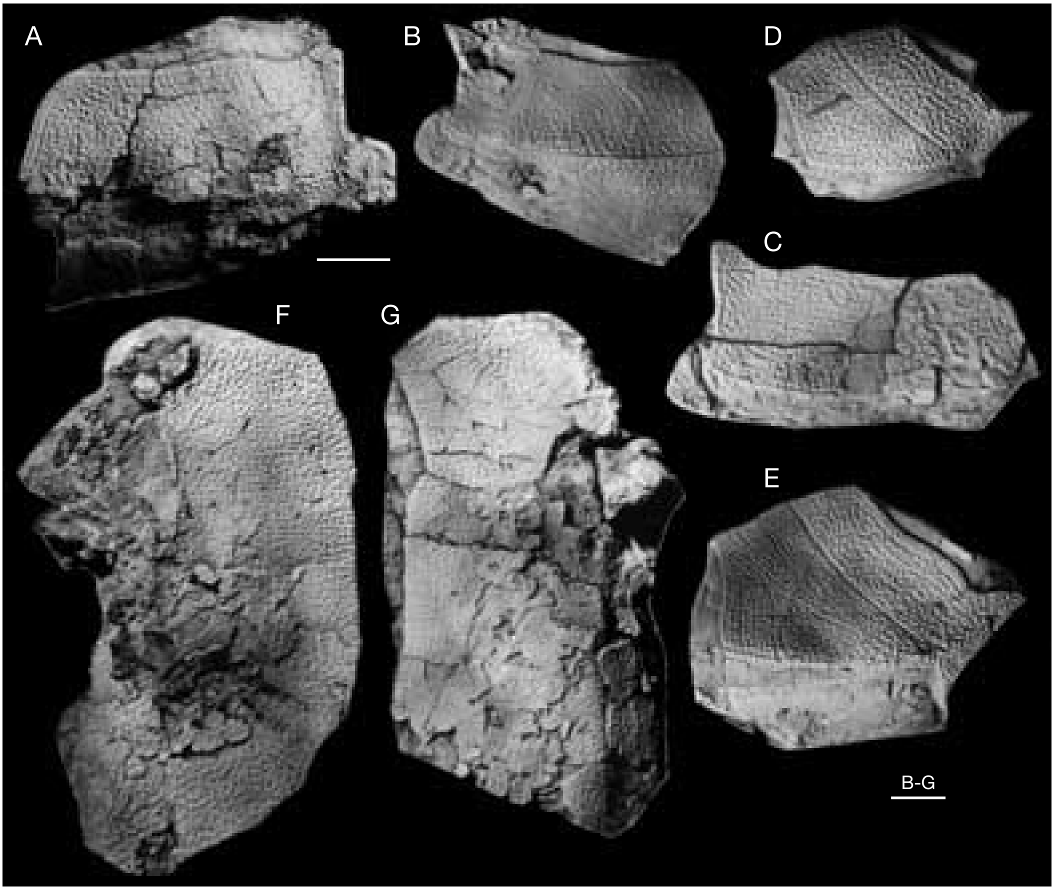

FIG. 37. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, ADL LDM 98/58; **B**, ADL LDM 89/12; **C**, ADL LDM 98/94; **D**, MxL LDM 98/54; **E**, MxL LDM 89/2; **F**, AVL LDM 89/7; **G**, AVL LDM 98/30. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AVL**, anterior ventro-lateral plate; **MxL**, mixilateral plate. Scale bars: 10 mm.

The PMD is broad in comparison with the AMD, B/L index about 95 in material from Scotland (Miles 1968) and varies from 88 to 101, 95 on the average, in material from Latvia. The anterior margin is very narrow, convex and rounded; the posterior margin is well convex, 2-2.5 times longer than the anterior margin; it is without pronounced posterior corner (Miles 1968: text-fig. 38; Fig. 35C; 36D).

The dorsal lamina of the ADL is of moderate breadth, 3.5 times as long as it is broad in RSM 1859.33.632D (Miles 1968: pl. 20, fig. 3) or a little broader in LDM 98/58 (Figs 36B; 37A). The postnuchal ornamented corner (pnoa) is large in all studied specimens.

The MxL was not described by Miles (1968) in details as being represented in Scottish material only by poorly preserved specimens. However, the dorsal lamina of the plate was correctly assumed by Miles (1968: 78) being slightly less than twice as long as it is broad. The dorsal corner is clearly seen. The lateral lamina is low, more than three times as long as it is broad. The posterior oblique sensory line groove (dlg2) usually terminates in some distance from the lateral margin; LDM 98/53 shows dlg2 crossing

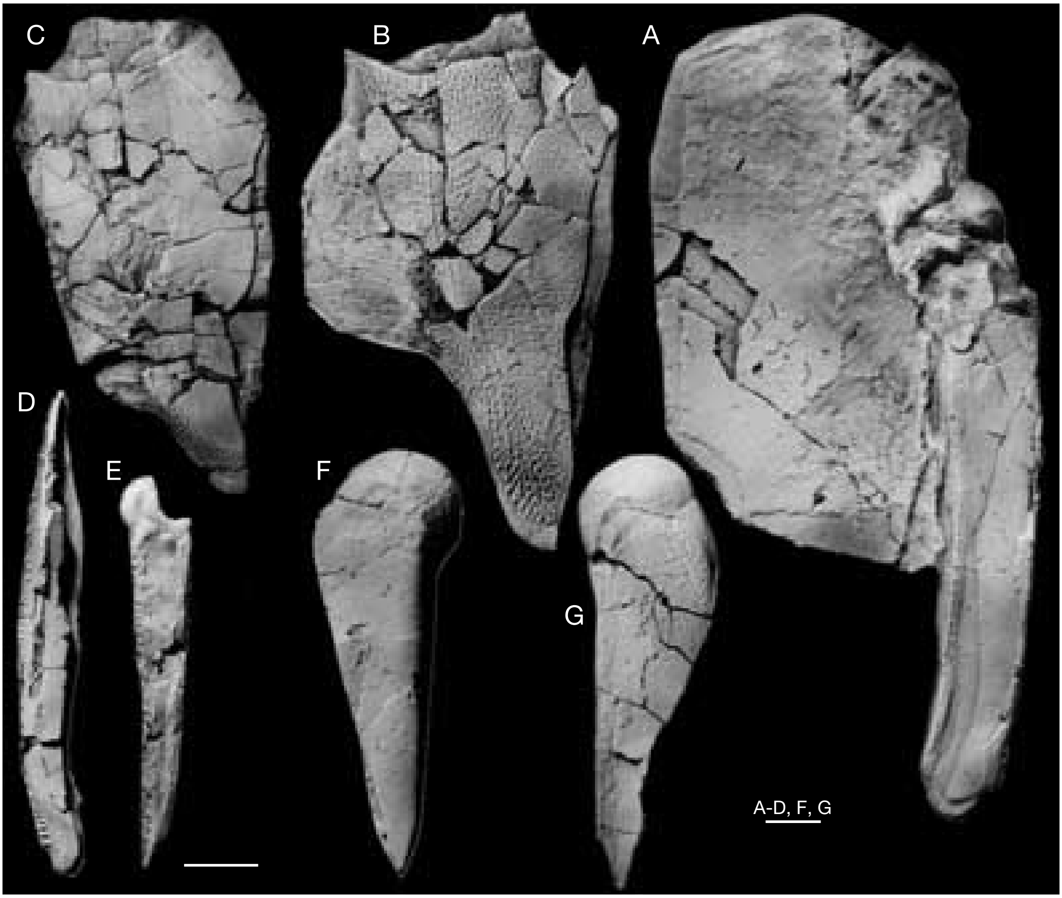

FIG. 38. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, AVL in visceral view with articulated proximal segment of pectoral fin LDM 98/78; **B**, PVL LDM 98/45; **C**, PVL LDM 98/41; **D**, ML2 LDM 98/76; **E**, distal segment of the pectoral fin LDM 89/4; **F**, CV1 LDM 98/90; **G**, CV1 LDM 98/77. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **CV1**, ventral central plate 1; **ML2**, lateral marginal plate 2; **PVL**, posterior ventro lateral plate. Scale bars: 10 mm.

the dorso-lateral ridge. In small specimen LDM 98/54 the dlg2 is connected with the main lateral line groove (lcg). The dorso-lateral ridge (dlr) is well-defined both in the ADL and MxL in material from Latvia; Miles (1968) claimed that "there is no clear development of the dlr on either the MxL or ADL"; in fact dlr is not clearly seen, particularly in MxL, because of preservation of the Scottish material as internal impressions.

The AVL with the ventral lamina is 1.9-2 times as long as it is broad; the anterior margin of the ventral lamina is rounded without clearly defined corners (Miles 1968: 79, text-fig. 39A; Figs 37F, G; 38A). The subcephalic division comprises 21-25% (22.5 on the average) of total length of the ventral lamina (about 20% in Scottish material: Miles 1968). The lateral lamina is not preserved within the material from Scotland. It is low, the ventral lamina 3.8 times as broad as the lateral lamina high in LDM 98/30. The lateral lamina is low. The right AVL overlaps the left AVL by very narrow overlap area.

The PVL has variable proportions. It is relatively narrow, the ventral lamina is 2.4-2.7 times as

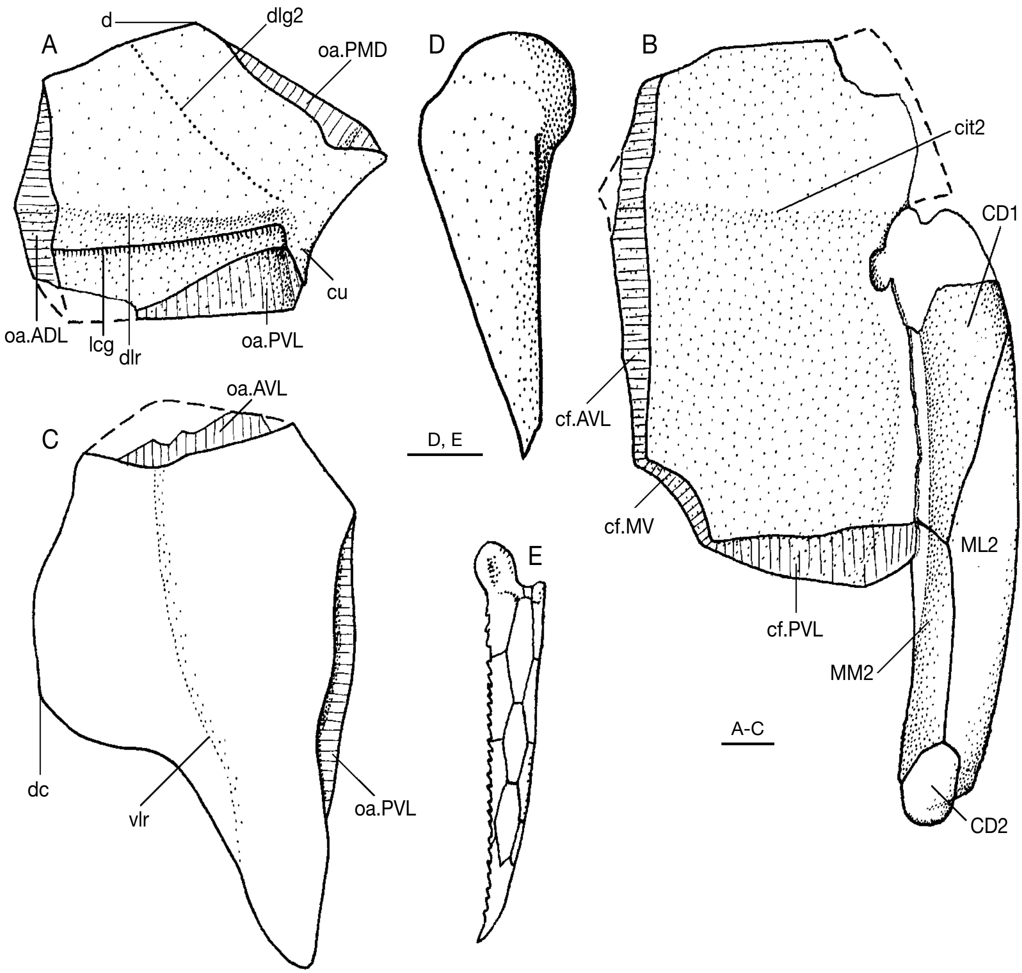

FIG. 39. — *Bothriolepis leptocheira curonica* Gross, 1942; **A**, MxL LDM 89/2; **B**, AVL plate in visceral view with articulated proximal segment of the pectoral fin in dorsal view LDM 98/78; **C**, PVL LDM 98/45 in ventral view; **D**, CV1 LDM 98/90; **E**, distal segment of the pectoral fin LDM 89/4. Amula River upstream Kalnamuiža watermill, Latvia. Eleja Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AVL**, anterior ventro-lateral plate; **CD1**, dorsal central plate 1; **CD2**, dorsal central plate 2; **CV1**, ventral central plate 1; **ML2**, lateral marginal plate 2; **MM2**, mesial marginal plate 2; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro lateral plate; **cf.AVL**, area overlapping AVL; **cf.MV**, area overlapping MV; **cf.PVL**, area overlapping PVL; **cit2**, transverse thickening on the visceral surface of AVL; **cu**, postero-ventral ornamented corner; **d**, dorsal corner of MxL; **dc**, dorsal corner of lateral lamina of PVL; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge; **lcg**, main lateral line groove; **oa.ADL**, area overlapped by ADL; **oa.AVL**, area overlapped by AVL; **oa.PMD**, area overlapped by PMD; **oa.PVL**, area overlapped by PVL; **vlr**, ventro-lateral ridge. Scale bars: 10 mm.

long as it is broad. The subanal division is narrow, it occupies about one fifth-one third (22-32%) of the total PVL length (Miles 1968: 80; Figs 38B, C; 39C). The lateral lamina is moderately high, 2.3-2.7 times long as it is high. The ventro-lateral ridge (vlr) is clearly defined both in the AVL and PVL.

The MV is not known, but the shape of the AVL and PVL suggest the small size of the slightly elongated MV.

The pectoral fin is represented in Latvian material by some disarticulated bones, and six specimens showing articulated plates of the proximal segment associated with the AVL. The proximal segment bears small rarely set lateral and mesial spines, the lateral spines are larger than the mesial ones; Miles (1968) suggested the mesial spines perhaps absent. The proximal segment is very long and narrow, it is 4.8-6 (5.5 on the average) times as long as it is broad (5.5 to 6 times as long as broad in Scottish material: Miles 1968: 80). The CD1 is of moderate size with L/B index varying from 2.7 to 3.7 (3.3 on the average). The CV1 is gently longer than the CD1 and slightly more elongate (L/B 3.4). The CD2 is slightly longer than it is broad. Specimen LDM 89/4 is an articulated distal segment. It is not adorned with marginal spines, the lateral spines are sharp and proximally directed. The distal segment is very long and narrow, L/B index 5.7. The CD5 plate is present in material from both countries.

The ornamentation is fine and basically of the reticular type (Miles 1968: 80), in quite large individuals from Latvia becoming smooth. The network of anastomosing ridges are broken into radially arranged shorter ridges on the head-shield plates. On the posterior margin of the PMD, subcephalic and subanal divisions the anastomoses between the ridges reduce and nodose short ridges are present. The ornamentation of the pectoral appendage is reticulate in general, on the anterior part of the CD1 and CV1 the ornament is radially arranged; in the distal part of the proximal segment the ornamentation became smooth. The longitudinal lineation in the ornament of the distal segment is well shown in LDM 89/4.

Remarks

This species was established by Traquair (1893) and well-described by Stensiö (1948) and Miles (1968). Gross (1942) erected *Bothriolepis curonica* as a new species from Latvia based on a slightly damaged head-shield LDM 15/32, two AMD and one PMD, and several fragments of pectoral fin bones collected in 1934 in the Bienes locality by student of geology Melderis. This description was repeated by Stensiö (1948) in Addenda to his monograph without further comments. Since then, the remains of this fish were collected by Sorokin & Lyarskaja in 1975, and expeditions of the Latvian Museum of Natural History in 1981-1982 in the Kalnamuiža locality. Later specimens described by Gross (1942), as well as a newly collected material from Kalnamuiža site were briefly described and figured (Lukševičs 1987), stressing the close morphological resemblance of *B. curonica* with *B. leptocheira* from Scotland. A direct comparison of the specimens belonging to these species during preparation of this work has indicated that they are conspecific. Nevertheless, there are several features which suggest than the Latvian material is a new subspecies of *Bothriolepis leptocheira*. *Bothriolepis leptocheira curonica* Gross, 1942 is morphologically very close to *Bothriolepis leptocheira leptocheira* from Scotland (Miles 1968). *B. leptocheira curonica* differs from the nominal subspecies in its 1) larger size; 2) more elongated AVL; 3) smoother ornamentation. The diagnosis of the species presented here is to the large extent based on that provided by Miles (1968), and description adds some previously not known details and comprises comparison of the material from Latvia with that from Scotland.

Discussion

Within other *Bothriolepis* from Scotland, Baltic and Russia, *Bothriolepis leptocheira* is particularly characterized by a very short orbital margin of the Prm, the long and narrow AMD and slender pectoral appendage (Miles 1968). Among the other species of *Bothriolepis*, *B. leptocheira* is morphologically closest to *B. jarviki* Stensiö, 1948 from Greenland (Stensiö 1948). Both species are similar in 1) their size; 2) shape and proportions of La and Nu of the head-shield; 3) the shape and proportions of the AMD; 4) the slender pectoral fin. However, *B. jarviki* differs from *B. leptocheira* in the other shape and proportions of the Prm, Pp, Nu, PMD and the ornamentation. *B. leptocheira* closely resembles also *B. jeremejewi* Rohon, 1900 from Timan by 1) the slender pectoral appendage; 2) the shape and proportions of the PMD; 3) smooth reticulate ornamentation. Unfortunately, *B. jeremejewi* is poorly described and known species, represented in collections of LDM and PIN by some badly preserved specimens showing disarticulated fragments of the PMD and pectoral fin. There is not yet enough information to decide whether these species are closely related or not.

Bothriolepis ornata Eichwald, 1840 (Figs 40-54)

Bothriolepis ornatus Eichwald 1840: 78.

Bothriolepis prisca – Eichwald 1840: 425.

Bothriolepis ornata – Eichwald 1860: 1513, pl. cvi, fig. 3.

Asterolepis ornata – Eichwald 1861: 448 (*p.p.*).

Bothriolepis cf. *ornata* Eichw. – Gross 1942: 403, 422 (*p.p.*) [non text-fig. 11].

For full list of synonyms before 1932, see Gross (1932).

Type specimen. — Woodward (1891) selected MM 116/107 as the lectotype (Eichwald 1860: 1513, pl. CVI, fig. 3). It is an AMD, collected by Helmersen.

Material examined. — From the type locality at Priksha River: MM 5/198, PVL; BMNH P.4600, ML1, P.710, MxL; PIN 835/4, Nu. From the locality at Skujaine River near Klūnas hamlet: LDM 43/730, 100/1-65, 145-147, 336, 346, 354-368, 396-426, 441, 523, 525-527, LGI 5/2045-2078, two articulated head-shields and their fragments, disarticulated plates of the head-shield, trunk-armour and pectoral appendage; PIN 1491/89, ADL, 1491/90-95, two Pn, two Sm, Pmg, CD2.

Localities and horizon. — The type locality is the exposure at Priksha River, Russia; the upper Famennian Lnyanka Beds. Other studied material comes from the two outcrops of white and pink sand containing abundant fish bones, dolomite marl and marl at the right bank of Skujaine River down Klūnas village, Latvia; the Famennian Tērvete Formation. Studied fragments of plates, undescribed here, which comes from Msta River near Beryozovik village (kept at IEC), and those reported from Belaya, Lnyanka and Mshanka Rivers in Novgorod region (Ostrometskaya & Kotlukova 1966; Obruchev 1964) and the North Timan, the Pokayama Formation (Obruchev 1958), probably also belong to *B. ornata*.

Diagnosis. — Rather large *Bothriolepis* with the dorsal length of the trunk-armour reaching 230-240 mm and the length of the head-shield at least 100 mm. B/L index of head-shield 127. Preorbital recess of trifid type. Orbital edges of Prm and La are thickened. Prm of moderate breadth, with B/L index about 112, rostral margin 1.7-1.9 times longer than orbital margin. Nu arched, narrow, with L/B index of 83. Pn narrow. B/L index of dorsal wall of trunk-armour about 82. Median dorsal ridge poorly developed. AMD moderately narrow, B/L index about 79-88. Anterior margin of AMD short and concave. PMD narrow, B/L index about 75-89, 82 on average. ADL with narrow lateral lamina and large postnuchal ornamented corner. Axillary foramen long and narrow. Proximal segment of the pectoral appendage moderately long, four times as long as broad. Ornamentation typically reticulate, in quite large individuals becoming coarser and sparser.

Description

Bothriolepis ornata is well-represented at the locality at the right bank of Skujaine River 1 km E from Klūnas hamlet by many disarticulated plates and some articulated skulls. Most are from well-grown individuals of moderate size, but there are also some small, and quite large specimens. *Bothriolepis ornata* is one of the largest of species of *Bothriolepis*, but did not quite reach the size of *B. maxima* or *B. gigantea*. The head-shield (Figs 40A-C; 42A, B) has a B/L index of about 127, and is strongly vaulted both rostrocaudally and transversely. The rostral margin is convex, slightly shorter than the posterior margin, which is weakly convex and bears a well-defined posterior median process. There are well-defined anterolateral corners (alc) and a deep prelateral notch (nprl). The obtected nuchal area (nm) is long, extending onto the Pn, it is broadest on the Nu. The orbital fenestra is relatively short and broad (B/L index about 200). Preorbital recess (prh) is distinctly trifid with extended lateral horns and a pointed median division, as in *B. maxima* and *B. hayi* Miles, 1968. The median division reached the middle of Prm, but lateral horns did not reach the middle of La, as is the case in *B. hayi*. The orbital edges of the Prm and La are thickened, as in *B. ciecere*, *B. macphersoni* and *B. karawaka*.

The visceral skull surface (Fig. 40B) shows the broad otico-occipital depression which is well-defined by the paramarginal cristae. The antero-

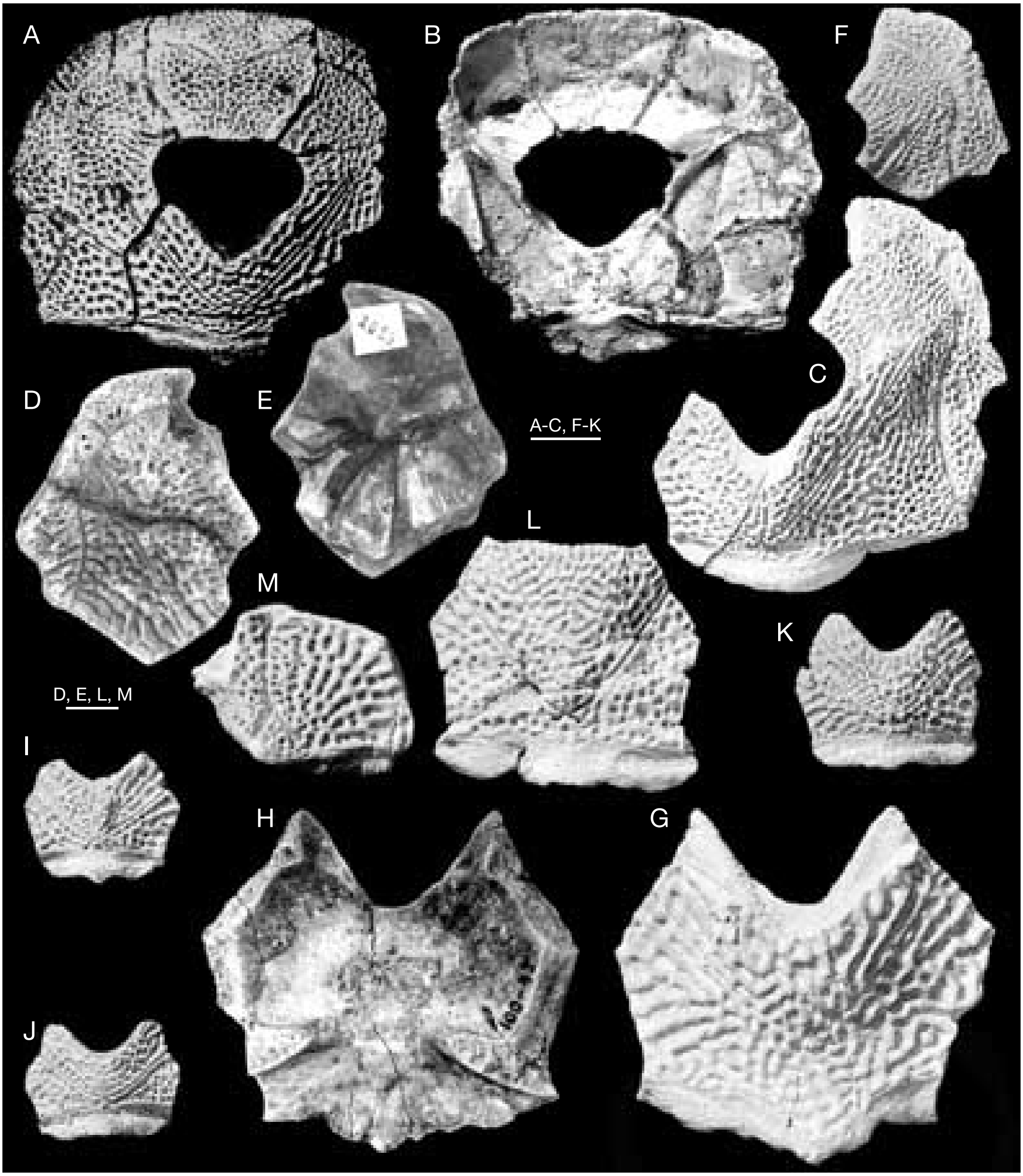

FIG. 40. — *Bothriolepis ornata* Eichwald, 1840; **A**, **B**, head-shield LDM 100/31 in dorsal and visceral views; **C**, head-shield LDM 100/32 in dorsal view; **D**, **E**, La LGI 5/2053 in dorsal and visceral views; **F**, La LDM 100/44; **G**, **H**, Nu LDM 100/42 in dorsal and visceral views; **I**, Nu LDM 100/39; **J**, Nu LDM 100/38; **K**, Nu LDM 100/399; **L**, articulated Nu and Pp LDM 100/398; **M**, Pn LDM 100/402. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate. Scale bars: 10 mm.

lateral corner of otico-occipital depression is broad in its base and extended nearly to the rostral margin of the orbital fenestra. The postero-lateral corner is rounded and does not extend laterally over the middle of the Pn's posterior margin, as it does in *B. ciecere*. The transverse

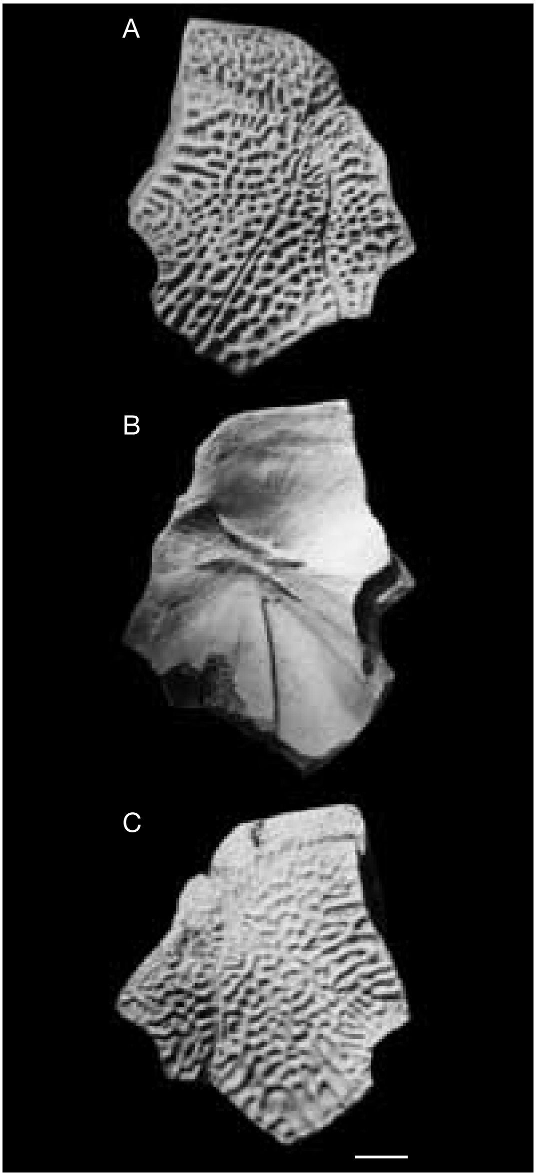

FIG. 41. — *Bothriolepis ornata* Eichwald, 1840, La plates; **A**, **B**, LDM 100/398 in dorsal and visceral views; **C**, LDM 100/525. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviation: **La**, lateral plate. Scale bar: 10 mm.

lateral groove is moderately broad and clearly defined. A relatively broad shallow depression anteriorly from the antero-lateral corner of preorbital recess is the lateral pit, which is situated more laterally than mesially. The median occipital crista is relatively low, often it consists from several small ridges. The transverse nuchal crista is prominent. The median ridge (mr) sharing the broad paired pits (g) of Pp plate is broad and anteriorly bears a tubercle. The supraotic thickening on the Nu is very low.

The Prm (Fig. 42C-E) is broadest slightly posteriorly from the infraorbital sensory groove. The rostral margin is convex, the orbital margin is straight or weakly concave and bears clearly defined but shallow nasal notch (pnn). The infraorbital sensory groove (ifc1) crosses the plate anteriorly from its middle part. The shape and proportions of the Prm resemble that in *B. ciecere*, differing well from that in such taxa as *B. leptocheira* and *B. maxima*.

The La (Figs 40D-F; 41; 43F) is moderately broad with L/B index about 123-139, 132 on the average. The rostral margin is relatively short and almost straight, the antero-median and antero-lateral corners are well-defined. The infraorbital sensory groove (ifc1) crosses the plate in its anterior part not far from the lateral margin. The central sensory line groove (csl) usually finishes slightly anteriorly the middle of an orbital fenestra length, it might be interrupted or very short.

The Pp (Figs 40L; 43A, B) is broad, L/B index varies from 56 to 83. As in other species the anterior margin is strongly convex in small specimens and became almost straight with increasing size.

The Nu (Figs 40G-L; 43C-E) is vaulted with an angle between right and left halves about 132°. It is relatively narrow, L/B index 72-93, 83 on the average, and in most aspects resembles that in *B. ciecere*. The anterior division of the lateral margin usually is concave and equal or a little longer than the posterior division. The posterior margin is weakly convex and bears well-defined median process (prnm). The orbital facetes are short, similarly as in *B. leptocheira* and *B. ciecere*. There are short supraoccipital grooves (socc), which terminate little in front of the obtected nuchal area at the external openings for the endolymphatic ducts (d.end). Specimen LDM 100/42 (Figs 40G; 43D) shows the broad

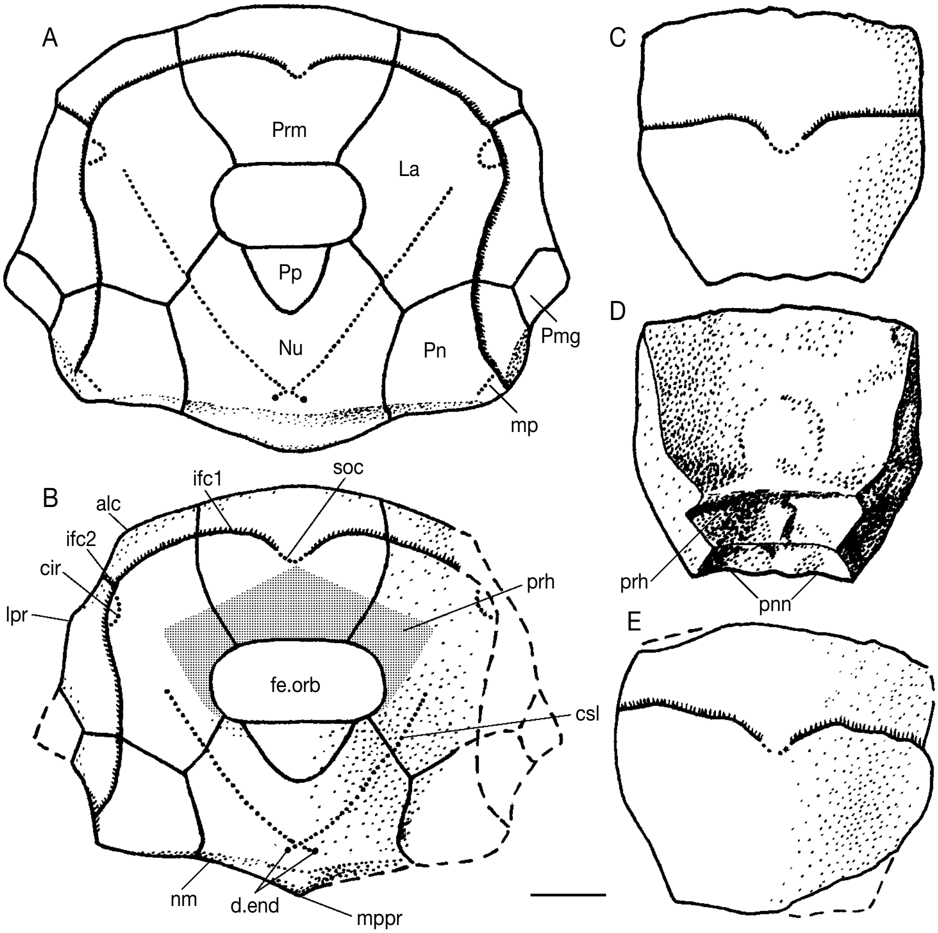

FIG. 42. — *Bothriolepis ornata* Eichwald, 1840; **A**, restoration of head-shield based on LDM 100/32; **B**, head-shield LDM 100/31; **C-E**, Prm; **C**, **D**, LDM 100/34 in dorsal and visceral views; **E**, LDM 100/396 in dorsal view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **alc**, antero-lateral angle of head-shield; **cir**, semicircular pit-line groove; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **fe.orb**, orbital fenestra; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **lpr**, lateral process of head-shield; **mp**, middle pit-line groove; **mppr**, posterior process; **nm**, obtected nuchal area; **pnn**, nasal notch; prh, preorbital recess; **soc**, anterior section of the supraorbital sensory line. Scale bar: 10 mm.

unornamented area along the postpineal notch, which probably was overlapped by the extremely broad Pp. As a result the outer surface of this Nu was excluded from contact with the orbital fenestra, as in *Asterolepis*.

The Pn (Figs 40M; 43H-J) with L/B index about 98. The lateral division of the Pn is relatively narrow and composing 50% of the breadth of a median division of the plate. The median division is as long as it is broad. The lateral margin of the plate is short. The Pn usually bears a short middle pit-line groove (mp).

The Sm (extralateral plate) is known from two badly preserved specimens PIN 1491/92 (Fig. 43G), and PIN 1491/93, both are the anterior end of the plate. The dorsal margin has a prominent antero-dorsal process (ad1). There is a groove (gr.sc) running along the dorsal margin

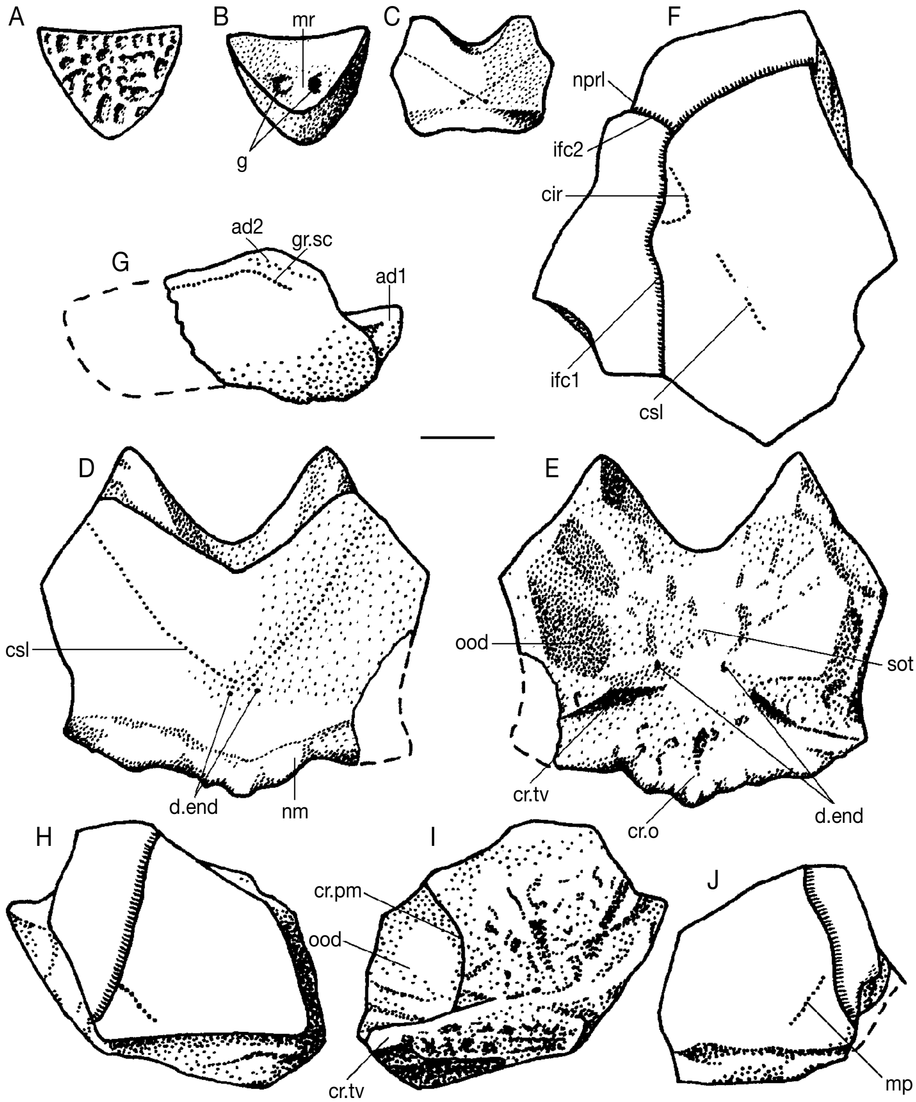

FIG. 43. — *Bothriolepis ornata* Eichwald, 1840; **A**, **B**, Pp LDM 100/41 in dorsal and visceral views; **C**-**E**, Nu; **C**, LDM 100/38 in dorsal view; **D**, **E**, LDM 100/42 in dorsal and visceral views; **F**, La LDM 100/358 in dorsal view; **G**, fragmentary Sm PIN 1491/92; **H**-**J**, Pn; **H**, **I**, PIN 1491/91 in dorsal and visceral views; **J**, PIN 1491/90 in dorsal view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **a2Sm**, posterior attachment area for submarginal plate; **ad1**, anterior articular process on submarginal plate; **ad2**, posterior articular process on submarginal plate; **cir**, semicircular pit-line groove; **cr.o**, median occipital crista; **cr.pm**, paramarginal crista; **cr.tv**, transverse nuchal crista; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **g**, paired pits on Pp; **gr.sc**, groove, possible for sensory canal; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **La**, lateral plate; **mp**, middle pit-line groove; **mr**, median ridge of Pp; **nm**, obtected nuchal area; **nprl**, prelateral notch; **Nu**, nuchal plate; **ood**, otico-occipital depression; **Pn**, paranuchal plate; **Pp**, postpineal plate; **pr.po**, antero-lateral corner of otico-occipital depression; **Sm**, submarginal plate; **sot**, supraotic thickening. Scale bar: 10 mm.

of the ornamented part of the plate, which is similar to that of *B. obrutschewi* (see Karatajūte-Talimaa 1966) and *B. macphersoni*.

The trunk-armour description is based on plasticine reconstruction composed of large disarticulated plates. The trunk-armour is relatively low and broad (B/L index 82), and broader than in *B. leptocheira* or *B. ciecere* (B/L index in both species about 77). Length of the dorsal wall probably exceeded 240 mm in largest individuals, but was only 50 mm in the smallest examined specimens. The dorsal wall is of moderate height, with right and left laminae enclosing an angle of about 132°. The median dorsal ridge is weakly defined, the dorsal wall is rounded transversely. The dorso-lateral and ventro-lateral ridges are well-defined, but in quite large individuals slightly rounded. The characteristic feature is that the depression anteriorly the tergal angle is weakly developed as in *B. groenlandica* Heintz, 1930 (see Stensiö 1948).

The AMD (Figs 44-46) with B/L index about 79-88, 83 on the average. The anterior margin is always concave. It is narrow, usually shorter than the posterior margin, and 2.2-3.1 times narrower as a total breadth of the plate, differing in its proportions from all the other species of *Bothriolepis* from the Famennian of Baltic area. The antero-lateral and lateral corners are rounded, the postnuchal notch (npn) is deep and postlevator process (pr.pl) is sharply defined. The posterior division of the lateral margin is 1.4-1.6 time shorter than the anterior division. There is no median dorsal ridge. Overlap areas for ADL and MxL are normally developed as usually in *Bothriolepis* in general, but in large individuals the sutural connection of AMD with MxL is often of *Remigolepis* type. The overlap area for ADL along the postnuchal notch is of wedge type: the outer surface of ADL slightly overlaps AMD. The anterior oblique dorsal sensory line groove (dlg1) is not present even in smallest specimen, the posterior oblique dorsal sensory line groove (dlg2) is well-defined also on the plates of rather large individuals. In some cases the posterior oblique dorsal sensory line groove is short: specimen LGI 5/2078 (Fig. 46H) shows dlg2 on the left side terminated in front of the postero-lateral margin.

The visceral surface of the AMD (Figs 44B; 45B, E; 46F) shows a narrow elongated levator fossa (f.retr), which is delineated by the low and narrow postlevator thickenings (alr). The supranuchal area (sna) is well-defined and broadest at the antero-lateral corners. The anterior ventral pit (pt1) is deep. The median ventral ridge (mvr) is high, it divides in the posterior third of the plate to form a deep median ventral groove (grm).

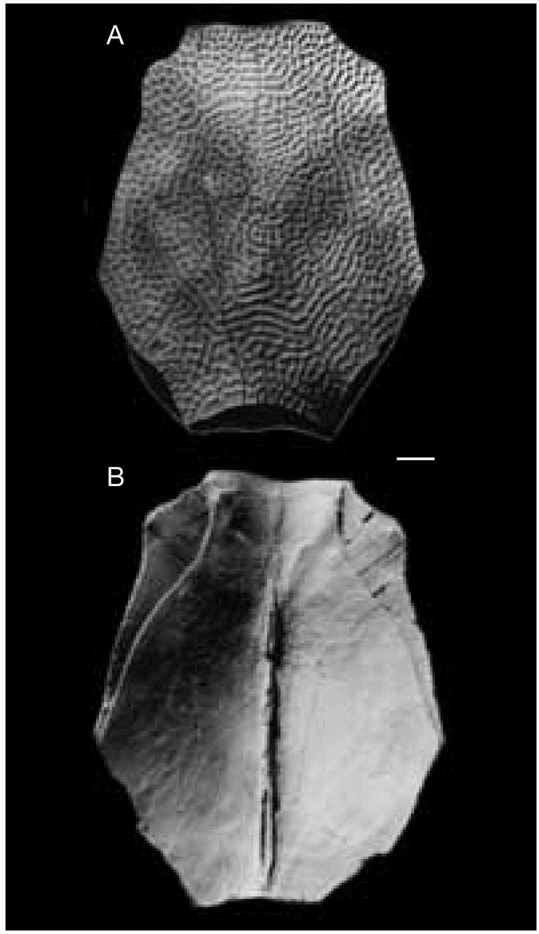

FIG. 44. — *Bothriolepis ornata* Eichwald, 1840, AMD LDM 100/2; **A**, dorsal view; **B**, visceral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviation: **AMD**, anterior median dorsal plate. Scale bar: 10 mm.

The anterior and posterior margins of the PDM (Figs 47-49A, B) both are strongly convex, with a well-developed anterior and posterior corners. The lateral and postero-lateral corners are also well-defined. The width of the anterior margin varies between 45-63% of total breadth of the

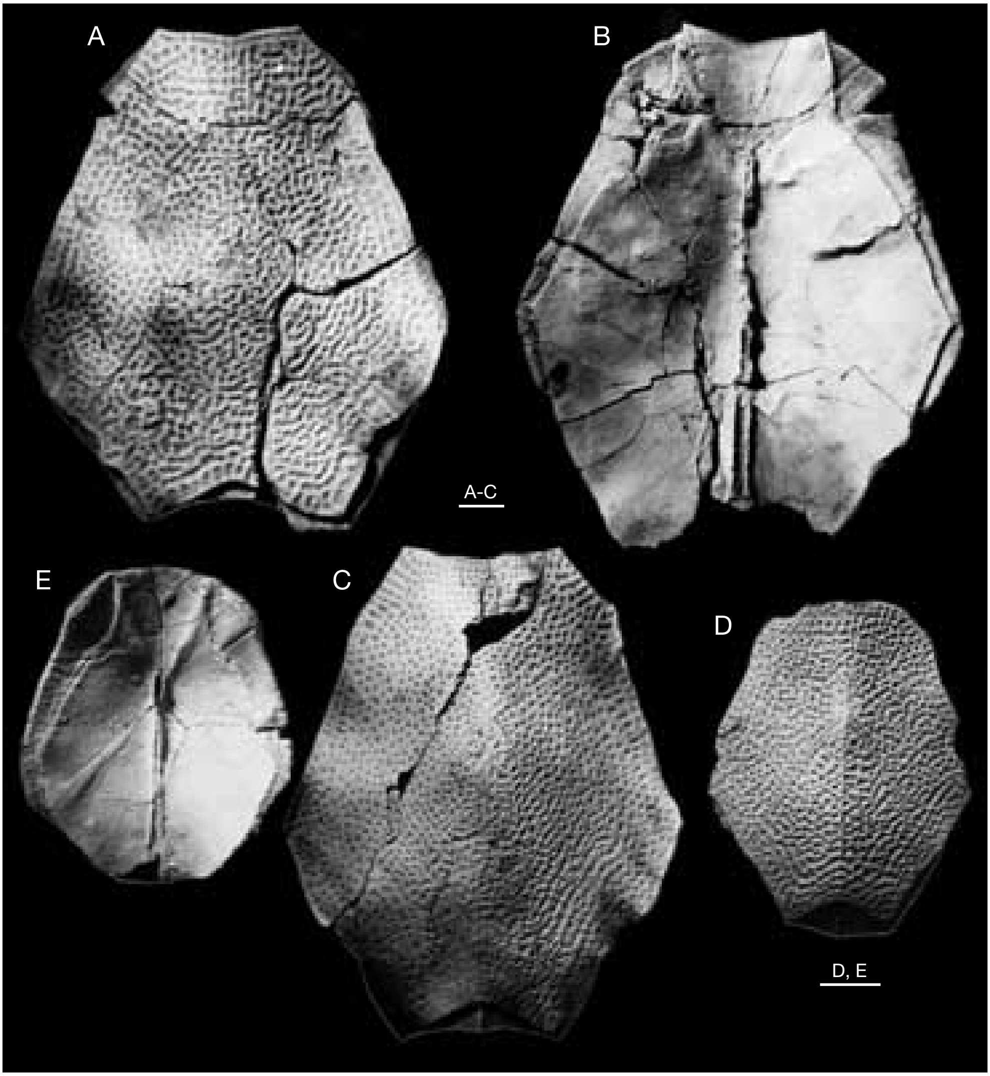

FIG. 45. — *Bothriolepis ornata* Eichwald, 1840, AMD; **A**, **B**, LDM 100/4 in dorsal and visceral views; **C**, LDM 100/527 in dorsal view; **D**, LDM 100/406 in dorsal view; **E**, LDM 100/405 in visceral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviation: **AMD**, anterior median dorsal plate. Scale bars: 10 mm.

plate. The PMD is arched with the median dorsal ridge (dmr) well-defined in individuals of small size; in large individuals the dmr is rounded. The suture with the MxL is of wedge type. The median ventral ridge and median ventral groove are weakly defined on the visceral surface of the plate in small individuals and the median ventral ridge is rather high with the deep posterior ventral pit (pt2) and strongly developed ventral tuberosity (tb) in large individuals (Fig. 48). The crista transversalis interna posterior (cr.tp) is low and smoothed, the postmarginal area (pma) being narrow.

The dorsal lamina (dlm) of the ADL (Figs 49C-E; 50A-C) is relatively long, but due to significant breadth of a strongly pronounced postnuchal

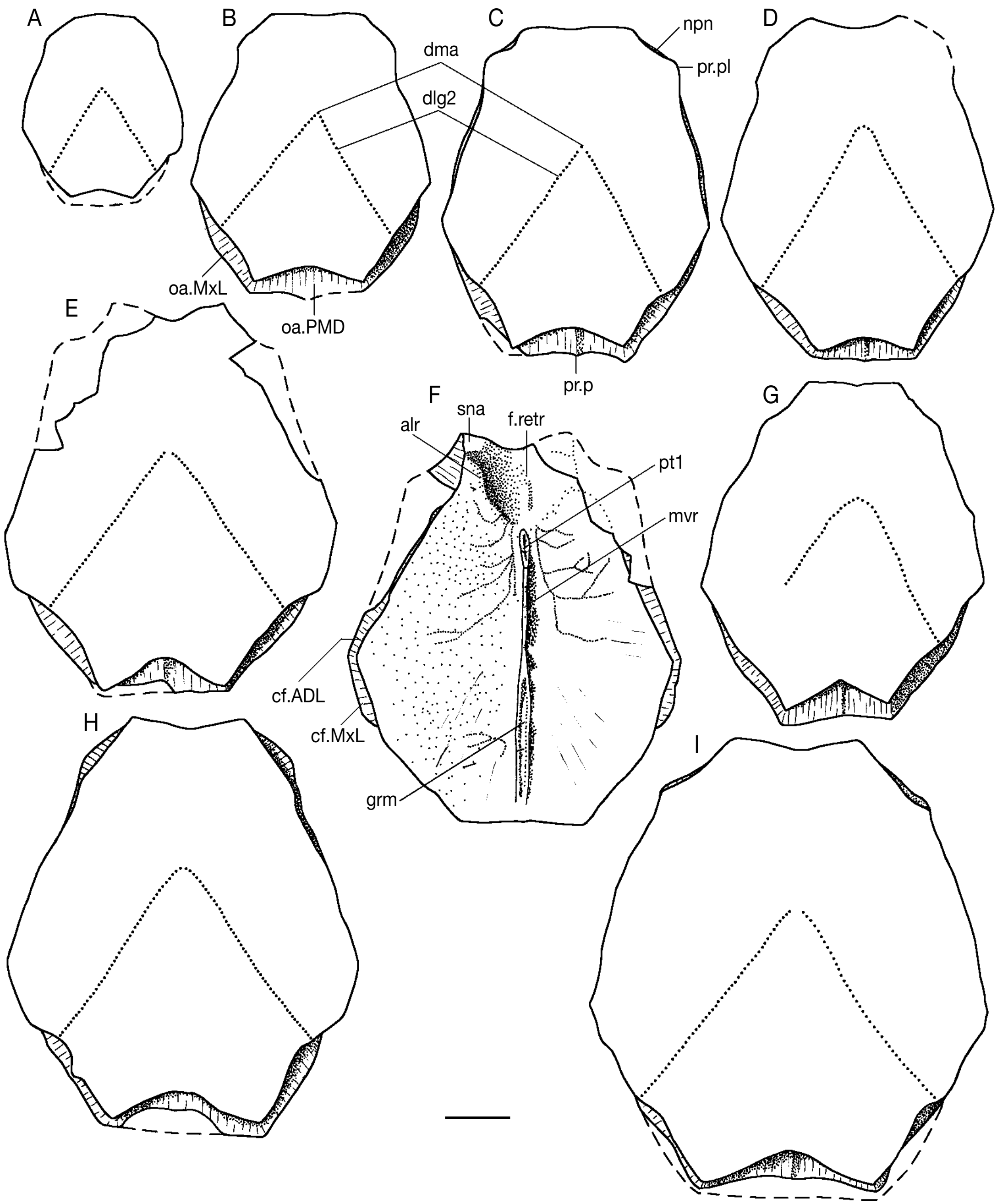

FIG. 46. — *Bothriolepis ornata* Eichwald, 1840, AMD; **A**-**E**, **G**-**I**, dorsal views; **F**, visceral view; **A**, LDM 100/405; **B**, LGI 5/2046; **C**, LDM 100/2; **D**, holotype MM 116/107; **E**, **F**, LDM 100/3; **G**, LDM 100/4; **H**, LGI 5/2078; **I**, LGI 5/2051; **A**-**C**, **E**-**I**, Skujaine River near Klūnas village, Latvia. Tērvete Formation; **D**, Prikscha River, Novgorod region, Lyubitino district, Russia. Lnyanka Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **alr**, postlevator thickenings of AMD; **cf.ADL**, area overlapping ADL; **cf.MxL**, area overlapping MxL; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **f.retr**, levator fossa; **grm**, ventral median groove; **mvr**, median ventral ridge; **npn**, postnuchal notch; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **prp**, posterior process of AMD; **pr.pl**, external postlevator process of AMD; **pt1**, anterior ventral pit; **sna**, supranuchal area of AMD. Scale bar: 20 mm.

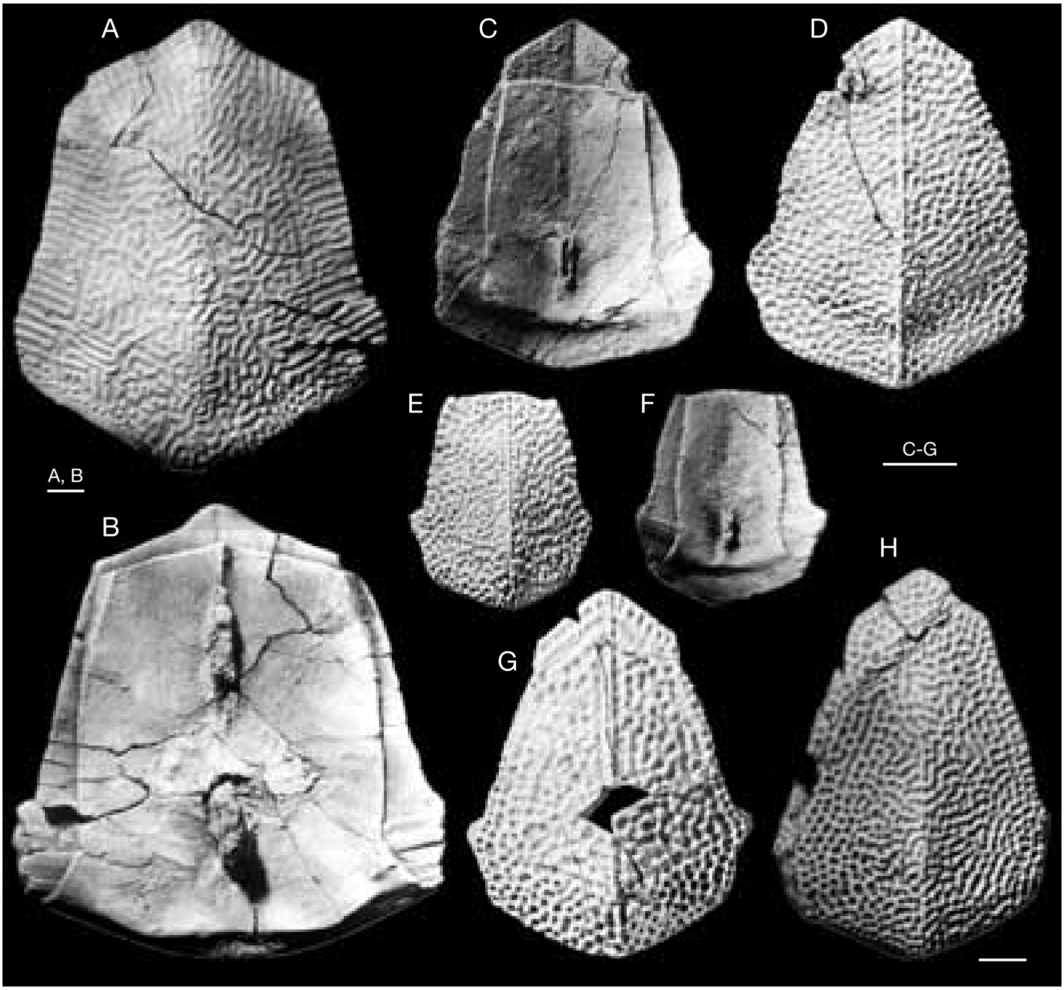

FIG. 47. — *Bothriolepis ornata* Eichwald, 1840, PMD; **A**, **B**, LDM 100/354 in dorsal and visceral views; **C**, **D**, LDM 100/356 in visceral and dorsal views; **E**, **F**, LDM 100/357 in dorsal and visceral views; **G**, LDM 100/355 in dorsal view; **H**, LDM 100/528 in dorsal view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviation: **PMD**, posterior median dorsal plate. Scale bars: 10 mm.

ornamented corner (pnoa) it is only 2.2 as long as it is broad. The lateral lamina is three times as long as it is high. The ADL is not simply overlapped by AVL, but also at the same time overlaps that plate posteriorly the processus obstans, as in *B. canadensis, B. groenlandica* and *B. maxima*.

The MxL (Figs 49F; 50D-F; 52A) is moderately broad. The dorsal lamina of the plate is less than twice (1.7-1.8 time) as long as it is broad. The lateral lamina is 2.5-2.6 times as long as it is broad, with long and sharp postero-ventral ornamented corner (cu).

The AVL (Figs 51A-C; 52D-E) is of moderate breadth, the ventral lamina of the single complete plate is 1.5 time as long as it is broad. The subcephalic division is of moderate length, comprises 29% of total length of the ventral lamina and has a weakly defined antero-lateral corner (c.al). The right AVL overlaps the left similar to the other *Bothriolepis*. The axillary foramen (f.ax) is rather large and about twice as long as it is broad (Fig. 51C). The processus brachialis shows some features not found in other *Bothriolepis* from the Main Devonian Field (Fig. 51D). The fossa articularis pectoralis is not boynded off anteriorly by the margo limitans. The groove around the external opening of the funnel pit (fp) is deep, its dorsal part is divided into two unequal deep pits; the larger and more distally situated pit bears an opening of the canal. Specimen LDM 100/365 (Figs 51D; 52E) shows the funnel pit divided into two divisions by very thin longitudinal wall. Probably this structure is the result of the joint desease.

The visceral surface of the AVL (Figs 51A; 52D) shows as in most part of other species of *Bothriolepis* the high transverse anterior crista (cit1) running antero-mesially and the low and broad transverse thickening (cit2) directed more mesially.

The PVL (Fig. 49G, H) is of moderate breadth, the ventral lamina is twice as long as it is broad. The subanal division is relatively narrow, it occupies about 30% of the total PVL length. The lateral lamina is about twice as long as it is high. Left PVL overlaps the opposite PVL.

The MV (Fig. 52B) is more elongated than in most species of *Bothriolepis*, the L/B index reaching about 1.4-1.7.

The pectoral fin is represented by many disarticulated bones (Figs 52F-I; 53), and two specimens showing articulated plates of the proximal segment associated with fragments of AVL (Fig. 54). There are three examples of the distal segments (Figs 52J; 53C, D). Both segments bear prominent lateral and mesial spines. The spines are large and closely setting on the proximal segment, in large individuals they are fusing at the base. The ventro-mesial margin is smoothed and rounded. The pectoral pit-line groove (sgp) is traced almost along the ventro-mesial margin and can be seen not on the MM2 as in *B. canadensis*, but on the CV1 and CV2 similar to *B. cristata* Traquair, 1895 and *B. ciecere*. The lateral spines of the distal segment are sharp and proximally directed, the

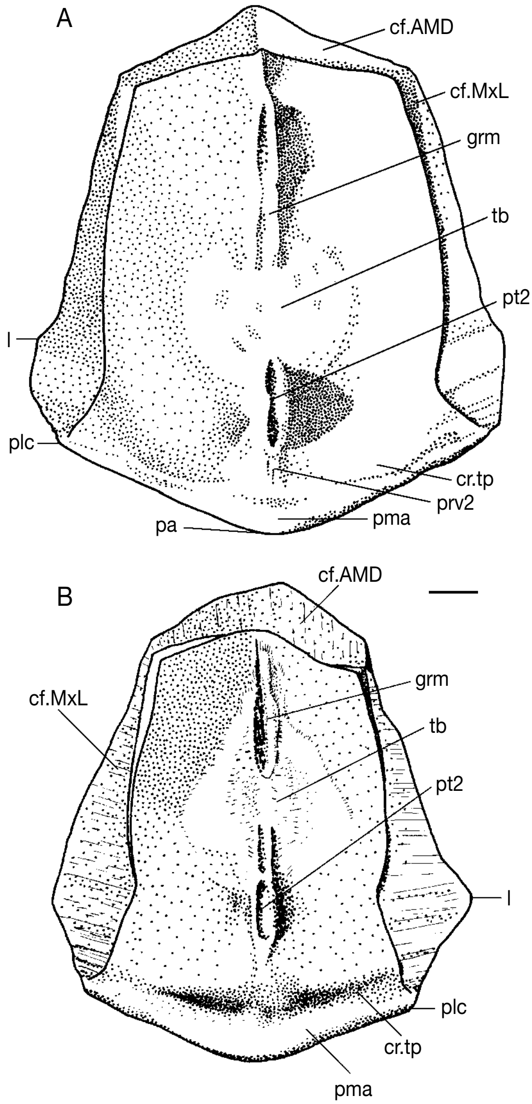

Fig. 48. — *Bothriolepis ornata* Eichwald, 1840, PMD in visceral view; **A**, LDM 100/354; **B**, LDM 100/408. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **cf.AMD**, area overlapping AMD; **cf.MxL**, area overlapping MxL; **cr.tp**, crista transversalis interna posterior; **dmr**, dorsal median ridge of trunk armour; **grm**, ventral median groove; **l**, lateral corner of PMD; **oa.MxL**, area overlapped by MxL; **pa**, posterior corner; **plc**, postero-lateral corner; **pma**, posterior marginal area; **prv2**, posterior ventral process of dorsal wall of trunk armour; **pt2**, posterior ventral pit; **tb**, ventral tuberosity. Scale bar: 10 mm.

mesial margin bears few rounded tubercles. The CD1 is moderately broad with L/B index about 2.7. The CV1 is slightly more elongate

FIG. 49. — *Bothriolepis ornata* Eichwald, 1840; **A**, **B**, PMD LDM 100/408 in dorsal and visceral views; **C**, ADL LDM 100/16; **D**, ADL LDM 100/412; **E**, ADL LDM 100/411; **F**, MxL LDM 100/21; **G**, PVL LDM 100/416; **H**, PVL LDM 100/27. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate. Scale bars: 10 mm.

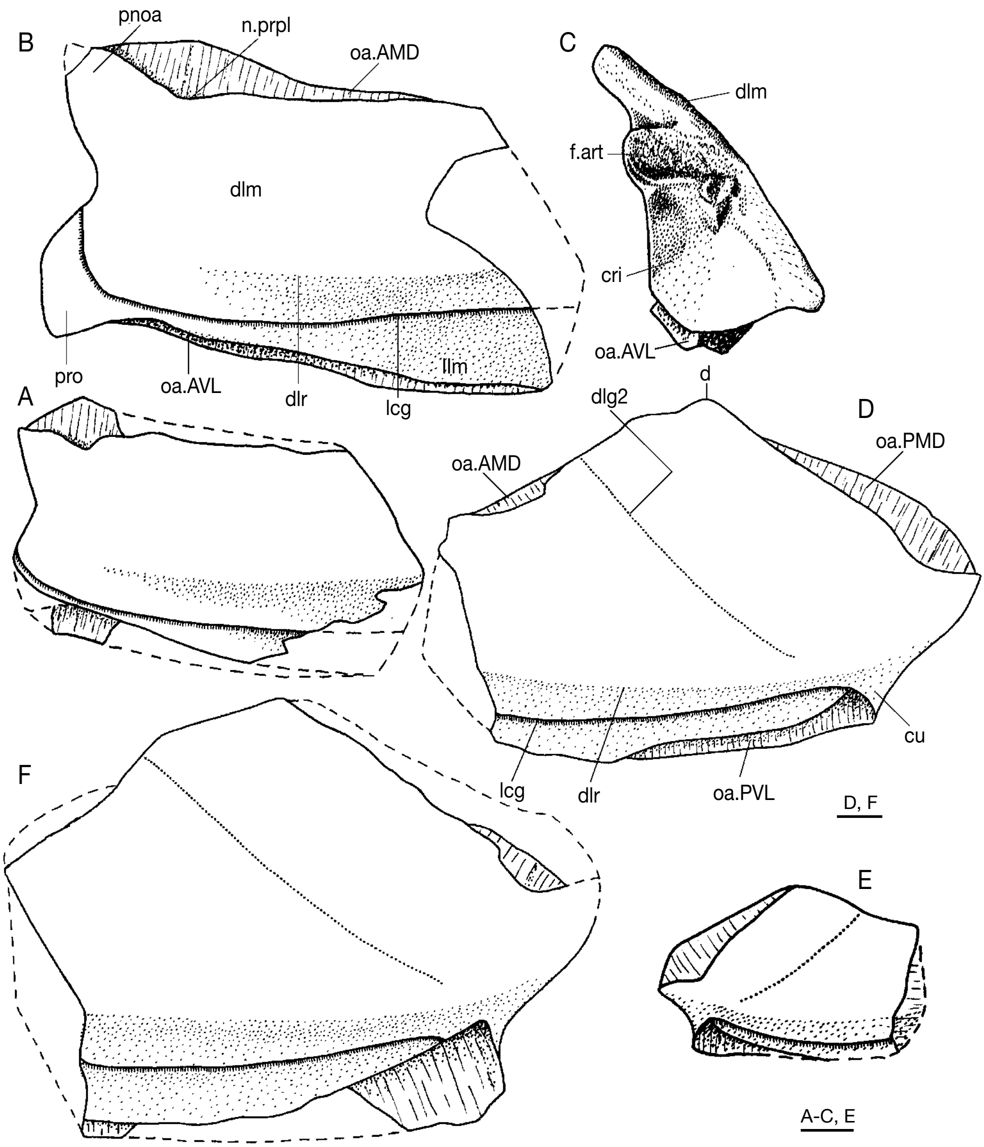

FIG. 50. — *Bothriolepis ornata* Eichwald, 1840; **A**-**C**, ADL; **A**, LDM 100/364 in dorsal view; **B**, LDM 100/16 in dorsal view; **C**, LDM 100/411 in anterior view; **D**-**F**, MxL; **D**, LGI 5/2058; **E**, LDM 100/21; **F**, LDM 100/20. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro lateral plate; **cri**, infra-articular crista; **cu**, postero-ventral ornamented corner; **d**, dorsal corner of MxL; **dlg2**, posterior oblique dorsal sensory line groove; **dlm**, dorsal lamina of ADL; **dlr**, dorso-lateral ridge; **f.art**, articular fossa; **lcg**, main lateral line groove; **llm**, lateral lamina of ADL; **n.prpl**, notch in dorsal margin of ADL for external postlevator process of AMD; **oa.AMD**, area overlapped by AMD; **oa.AVL**, area overlapped by AVL; **oa.PMD**, area overlapped by PMD; **oa.PVL**, area overlapped by PVL; **pnoa**, postnuchal ornamented corner; **pro**, processus obstans. Scale bars: 10 mm.

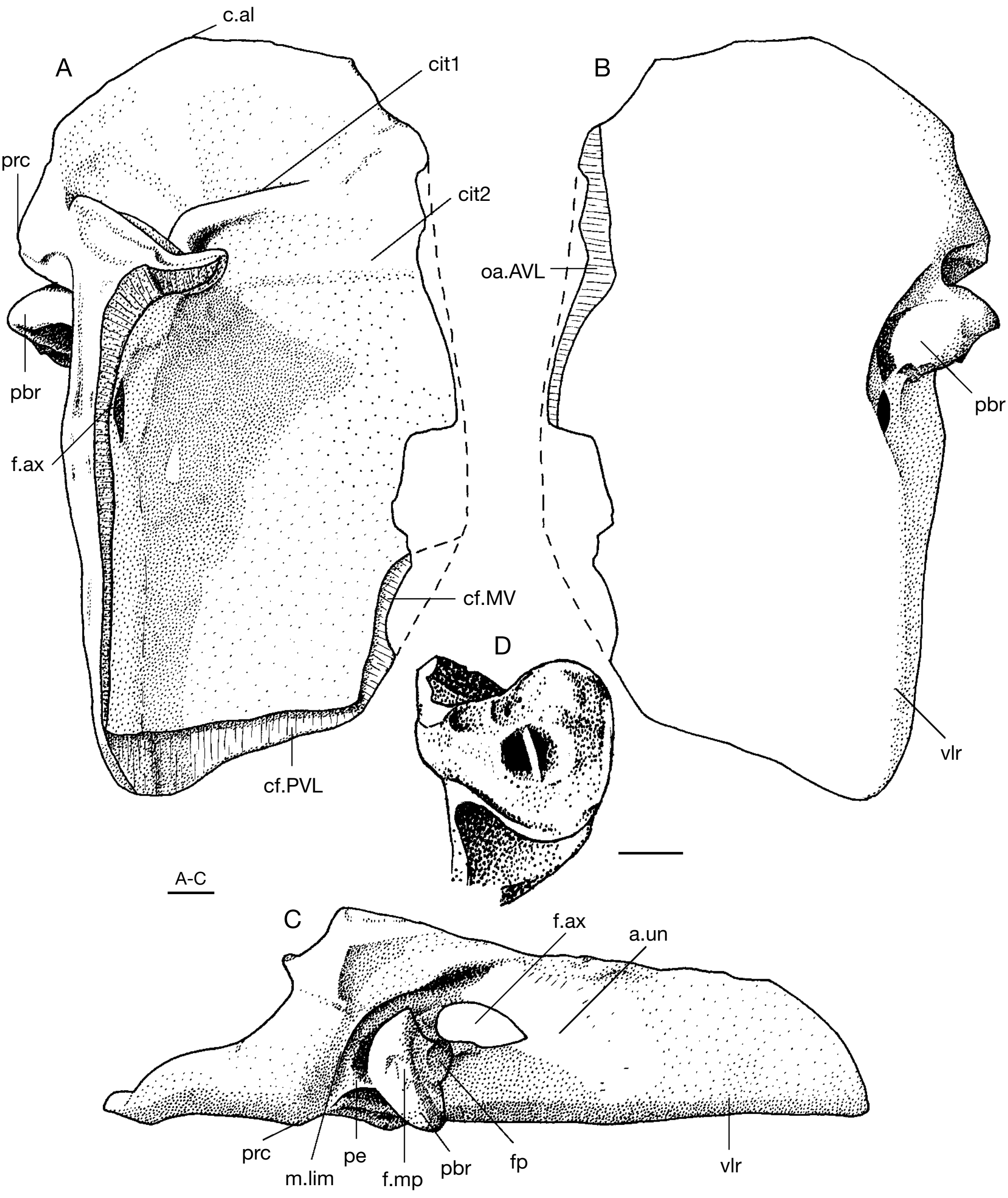

FIG. 51. — *Bothriolepis ornata* Eichwald, 1840; **A-C**, AVL LDM 100/414; **A**, visceral view; **B**, ventral view; **C**, lateral view; **D**, disarticulated processus brachialis of the AVL LDM 100/365. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **MxL**, mixilateral plate; **PVL**, posterior ventro lateral plate; **a.un**, unornamented area beneath fossa articularis pectoralis; **c.al**, antero-lateral corner of subcephalic division; **cf.MV**, area overlapping MV; **cf.MxL**, area overlapping MxL; **cf.PVL**, area overlapping PVL; **cit1**, crista transversalis interna anterior; **cit2**, transverse thickening; **f.ax**, axillary foramen; **f.mp**, protractor area; **fp**, funnel pit; **m.lim**, margo limitans of AVL; **oa.AVL**, area overlapped by AVL; **p.br**, processus brachialis; **pe**, pars pedalis; **prc**, prepectoral corner; **vlr**, ventro-lateral ridge. Scale bars: 10 mm.

FIG. 52. — *Bothriolepis ornata* Eichwald, 1840; **A**, MxL LDM 100/20; **B**, MV LDM 100/30; **C**, disarticulated *processus brachialis* of the AVL LDM 100/365; **D**, **E**, AVL LDM 100/414 in visceral and ventral views; **F**, CD2 LDM 100/424; **G**, CD1 LDM 100/418; **H**, CD1 LDM 100/417; **I**, CV1 LDM 100/421; **J**, distal segment of pectoral fin LDM 100/45. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **CD1**, **2**, dorsal central plates 1 and 2; **CV1**, ventral central plate 1; **MV**, median ventral plate; **MxL**, mixilateral plate. Scale bars: 10 mm.

than the CD1 (L/B 3.1). The CD2 is slightly longer than broad. The CV2 is 4.5-5.1 times as long as it is broad. The distal segment is normally developed, showing the CD3 and CD4, but CD5, which is well-defined in *B. leptocheira*, in *B. ornata* is not present.

The ornamentation is typically reticulate, in quite large individuals becoming coarser and sparser. The network of anastomosing ridges in large individuals is broken into irregular ridges, but never into short ridges or tubercles. The irregular ridges are situated without any order,

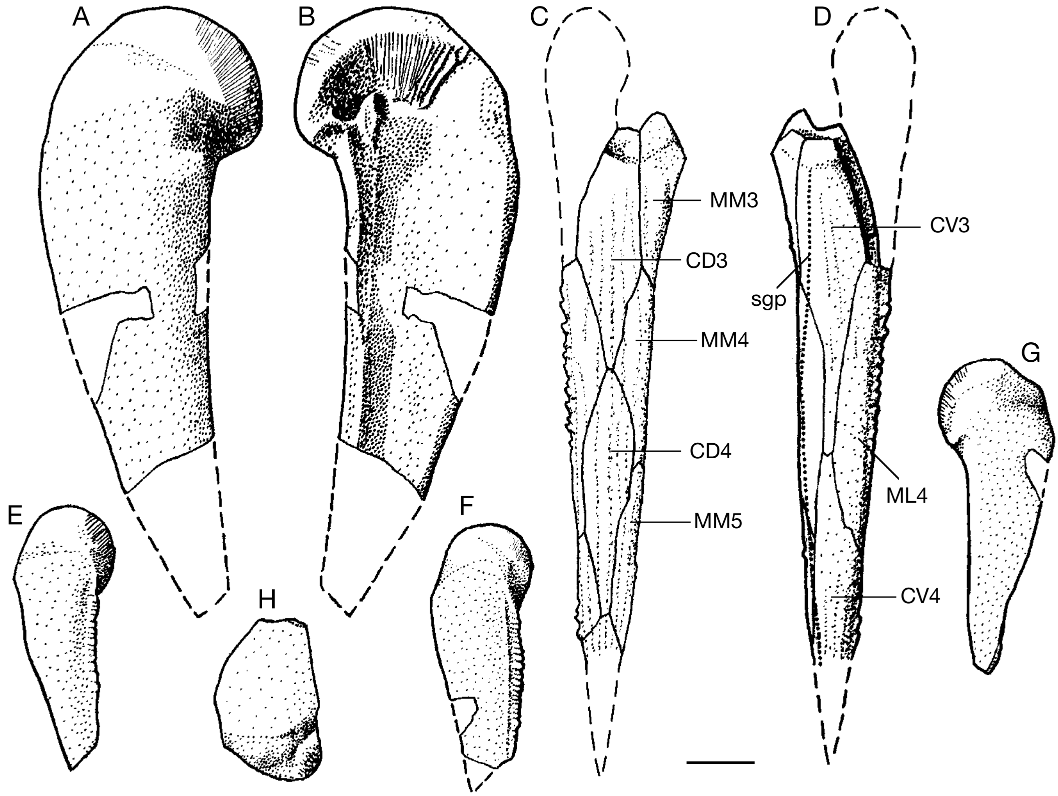

FIG. 53. — *Bothriolepis ornata* Eichwald, 1840; **A**, **B**, CV1 LDM 100/422 in dorsal and ventral views; **C**, **D**, distal segment of the pectoral fin LDM 100/45 in ventral and dorsal views; **E**, CD1 LDM 100/418 in dorsal view; **F**, CD1 LDM 100/419 in dorsal view; **G**, CV1 LDM 100/421 in dorsal view; **H**, CD2 LDM 100/424 in dorsal view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **CD1-4**, dorsal central plates 1 to 4; **CV1**, **3**, **4**, ventral central plates 1, 3 and 4; **ML4**, lateral marginal plate 4; **MM3**-**5**, mesial marginal plates 3, 4 and 5; **sgp**, pectoral pit-line groove. Scale bar: 10 mm.

only one specimen of PMD shows ridges perpendicular to margins of the plate. The ornamentation of the pectoral appendage remains reticulate even in quite lagre individuals. The distal segment ornament consists of low longitudinal ridges, which are weakly defined on the ventral surface and more distinct on the dorsal surface of the segment.

REMARKS

Bothriolepis ornata was introduced by Eichwald (1840) for specimen of the AMD collected by Helmersen at Priksha River (as indicated on the label), tributary of Msta River, near Borovichi town in the Novgorod region. The lectotype and four other specimen from the type locality (collected by H. Helmersen, A. Olivieri & R. Hecker) were studied in details and compared with the material from Skujaine River, Latvia, collected by the author (hold in LDM) and Karatajūte-Talimaa (kept in LGI and PIN), and attributed to the same species by Lukševičs (1992). The following account is the first full treatment in English, all materials from the type locality and Latvia are described here.

DISCUSSION

Bothriolepis ornata at the Skujaine locality is associated with *B. jani* (Lukševičs 1986). *B. ornata* can be distinguished readily from *B. jani* by its 1) larger size; 2) typical reticulate ornament, which is tubercular in *B. jani*;

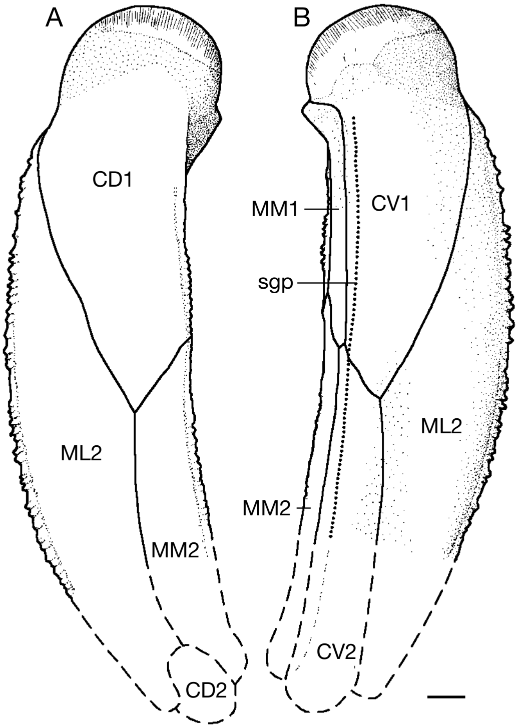

FIG. 54. — *Bothriolepis ornata* Eichwald, 1840, proximal segment of the pectoral appendage LGI 5/2050A; **A**, dorsal view; **B**, ventral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **CD1**, **2**, dorsal central plates 1 and 2; **CV1**, **2**, ventral central plates 1 and 2; **ML2**, lateral marginal plate 2; **MM1**, mesial marginal plate 1; **MM2**, mesial marginal plate 2; **sgp**, pectoral pit-line groove. Scale bar: 10 mm.

3) shape and proportions of almost all trunk-armour plates. *B. ornata* also resembles *B. ciecere* by some features (see description of *B. ciecere* for comparisons).

Bothriolepis hayi is a species that most resembles *B. ornata* among Scottish *Bothriolepis*. *B. ornata* differs from *B. hayi* most strikingly in the larger size and the narrower AMD and PMD, but also in the proportions of the Prm, La, Nu, Pn and more broad postnuchal ornamented corner of the ADL.

B. ornata is morphologically close to *B. groenlandica* (Stensiö 1948). The two species are of similar size, and have similar proportions and shape of almost all the head-shield, trunk-armour and pectoral appendage plates. The distinctions between them are insignificant and consist in that in *B. ornata* 1) the head-shield is slightly narrower and more arched; 2) the La and Pn are narrower; 3) the rostral margin of the La is shorter; 4) the mesial division of the Pn is of different shape. These could be intraspecific variations or preservation differences, but direct comparison of the Baltic and Greenland material is needed to solve this problem.

Bothriolepis jani Lukševičs, 1986
(Figs 55-61)

Bothriolepis jani Lukševičs, 1986: 131, pl. 1, fig. 8.

HOLOTYPE. — Right MxL LDM 100/88.

MATERIAL EXAMINED. — LDM 100/526, articulated head-shield, LDM 100/66-108, 100/119-122, 100/137, 100/148, 100/374-377, 100/431-434, disarticulated plates of the trunk armour; 100/109-118, 100/123-136, 100/370, 100/371, 100/378, 100/435-440, plates of the pectoral appendage; 100/144, 100/427, 2 Prm; 100/369, 100/428, 2 La; 100/429, LGI 5/2028, 2 Pp; LDM 100/138-143, 100/372, 100/430, 8 Nu.

LOCALITIES AND HORIZON. — The type locality is an exposure of white and pink sandstone containing abundant fish bones, dolomite marl and marl at the right bank of Skujaine River down Klūnas village (number 8 in Fig. 1); the Famennian Tērvete Formation. Other material comes from an outcrop of red and pink sandstone at the right bank of Svēte River near Ķurbes hamlet (number 9 in Fig. 1); the Mūri Formation.

DIAGNOSIS. — Small *Bothriolepis* with a median dorsal armour length reaching about 65 mm. B/L index of trunk-armour about 90. Prm broad, posterior margin is slightly shorter than almost straight anterior margin. Nu strongly arched, L/B index of 59; AMD strongly arched, B/L index 97. Anterior margin of AMD is broad, posterior margin of AMD and anterior margin of PMD are narrow. Median dorsal ridge strongly developed. Lateral line sensory groove terminates on posterior margin of the MxL. Proximal segment of pectoral appendage three times as long as broad, with prominent lateral and mesial spines. Ornamentation reticulate in small individuals and typically tuberculate in well-grown individuals, consisting of numerous closely irregularly set rounded tubercles.

DESCRIPTION

This species is represented mainly by disarticulated plates, single articulated, but slightly

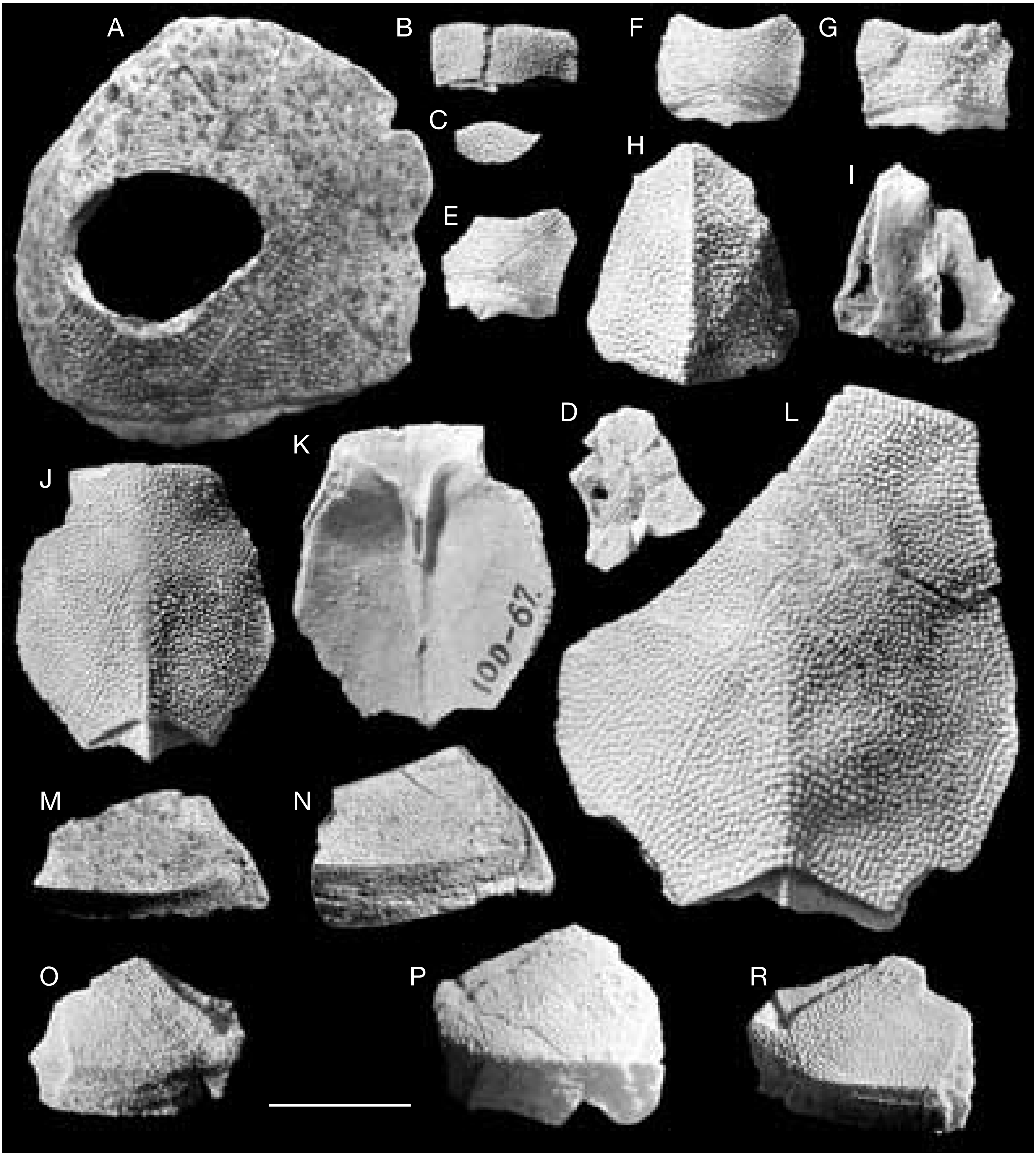

FIG. 55. — *Bothriolepis jani* Lukševičs, 1986; **A**, head-shield 100/526 in dorsal view; **B**, Prm LDM 100/144; **C**, Pp LDM 100/429; **D**, La LDM 100/369; **E**, Nu LDM 100/141; **F**, paratype, Nu LDM 100/142; **G**, Nu LDM 100/430; **H**, PMD LDM 100/83; **I**, PMD LDM 100/76 in visceral view; **J**, **K**, paratype, AMD LDM 100/67 in dorsal and visceral views; **L**, AMD LDM 100/431; **M**, ADL LDM 100/121; **N**, ADL LDM 100/122; **O**, MxL LDM 100/432; **P**, MxL 100/377; **R**, holotype, MxL LDM 100/88. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate. Scale bar: 10 mm.

deformed head-shield and a single articulated proximal segment of the pectoral fin. The head-shield (Figs 55A; 56A) has an estimated B/L index of about 127, and is strongly vaulted both rostrocaudally and transversely. The rostral margin is convex, shorter than the posterior margin, which is straight and bears a well-defined posterior median process. The antero-lateral corners and shallow prelateral notch are well-defined. The obtected nuchal area is long, extending onto the Pn, it is broadest on the Nu. The orbital fenestra is relatively large (B/L index about 176). The preorbital recess is of pentagonal type.

The Prm is broad, B/L index of about 116, arched, with an almost straight rostral margin, as in LDM 100/144, which is an anterior division of the Prm (Fig. 55B). LDM 100/427 is a more complete smaller Prm (Fig. 56B) which is more arched, and broadest at the rostral margin. The rostral margin more than twice longer than the concave orbital margin. The infraorbital sensory groove crosses the plate far from the rostral margin, unlikely that in *B. ornata*. The anterior section of the supraorbital sensory line is not recognized.

The La (Fig. 55D) is broad with L/B index of about 136-137 (n = 2). The rostral margin is of moderate breadth and almost straight. The infraorbital sensory groove crosses the plate almost in its middle part far from the orbital and lateral margins. The central sensory line groove (csl) extends slightly past the middle of the orbital fenestra. The antero-lateral corner of the otico-occipital depression on the visceral surface is relatively narrow and extends forward at the level of the middle of orbital fenestra length. The preorbital recess is not clearly seen, but the outlines on the visceral surface of specimen LDM 100/369 allows to suggest that it could be of trifid type.

The very broad Pp (LDM 100/429: Figs 55; 56C, and LGI 5/2028) has a strongly convex anterior margin. A narrow median ridge (mr) separates the deep paired pits (g) on the visceral surface of the plate. Both specimen clearly differ from the Pp of similar size (LDM 100/373) of *B. ornata* which comes from the same locality, by their tubercular ornament and broader general proportions.

The Nu (Figs 55E-G; 56D-G) is strongly arched with an angle between right and left halves about 103-125°. It is relatively short and broad

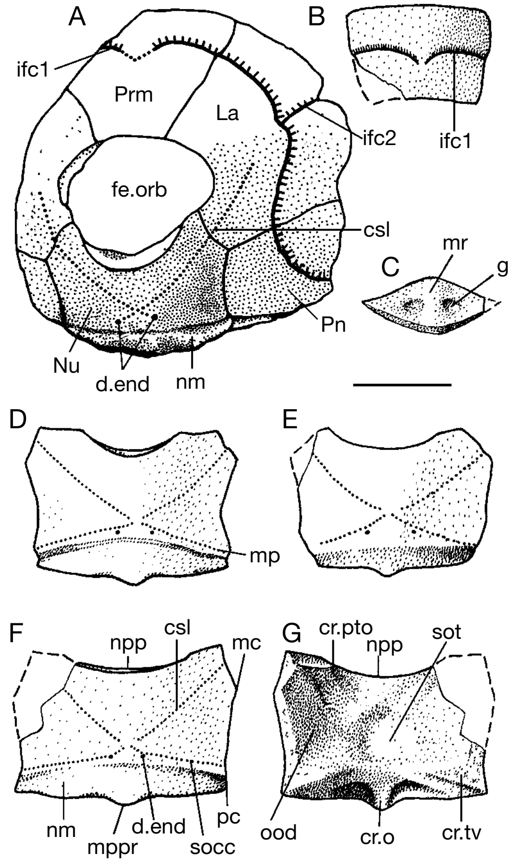

Fig. 56. — *Bothriolepis jani* Lukševičs, 1986; **A**, head-shield LDM 100/526; **B**, Prm LDM 100/427; **C**, Pp LDM 100/429 in visceral view; **D**-**G**, Nu; **D**, LDM 100/430 in dorsal view; **E**, LDM 100/142 in dorsal view; **F**, **G**, LDM 100/372 in dorsal and visceral views. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prm**, premedian plate; **cr.o**, median occipital crista; **cr.pto**, postorbital crista; **cr.tv**, transverse nuchal crista; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **fe.orb**, orbital fenestra; **g**, paired pits on Pp; **ifc1**, principal section of infraorbital sensory line on head-shield; **ifc2**, branch of infraorbital sensory line diverging on La; **mc**, lateral corner; **mp**, middle pit-line groove; **mppr**, posterior process on Nu; **mr**, median ridge of Pp; **nm**, obtected nuchal area; **npp**, postpineal notch; **ood**, otico-occipital depression; **pc**, postero-lateral corner; **socc**, supraoccipital cross-commissural pit-line groove; **sot**, supraotic thickening. Scale bar: 5 mm.

(L/B index 57-63, 59 on the average). The anterior division of the lateral margin is much shorter than the posterior division. The obtected nuchal area (nm) is relatively long, it extends on the Pn. In specimens LDM 100/140 and 100/372

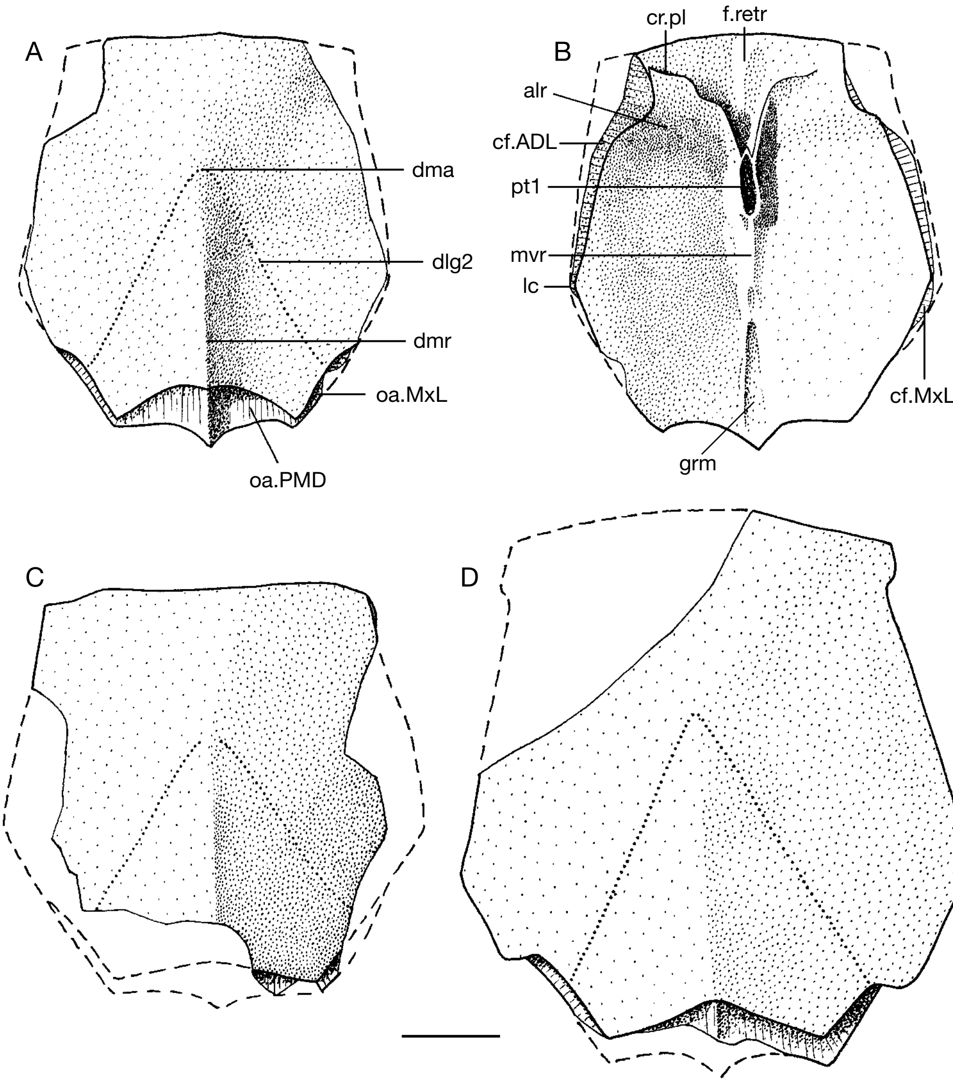

FIG. 57. — *Bothriolepis jani* Lukševičs, 1986, AMD; **A**, **B**, LDM 100/67 in dorsal and visceral views; **C**, LDM 100/119 in dorsal view; **D**, LDM 100/431 in dorsal view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **alr**, postlevator thickenings; **cf.ADL**, area overlapping ADL; **cf.MxL**, area overlapping MxL; **cr.pl**, postlevator crista; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **dmr**, dorsal median ridge; **f.retr**, levator fossa; **grm**, ventral median groove; **lc**, lateral corner; **mvr**, median ventral ridge; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **pt1**, anterior ventral pit. Scale bar: 5 mm.

(Fig. 56F), there are supraoccipital grooves (socc) which terminate little in front of the obtected nuchal area at the large external openings for the endolymphatic ducts (d.end). Specimens LDM 100/141, 100/142, 100/430 (Figs 55E-G; 56D-E), and 100/527 show well-defined middle pit-line grooves (mp), which are not connected with endolymphatic opening and extend to the lateral margin of the plate. The median occipital crista (cr.o) and the transverse nuchal crista are well-defined. The postorbital crista (cr.pto) on the visceral surface is weakly

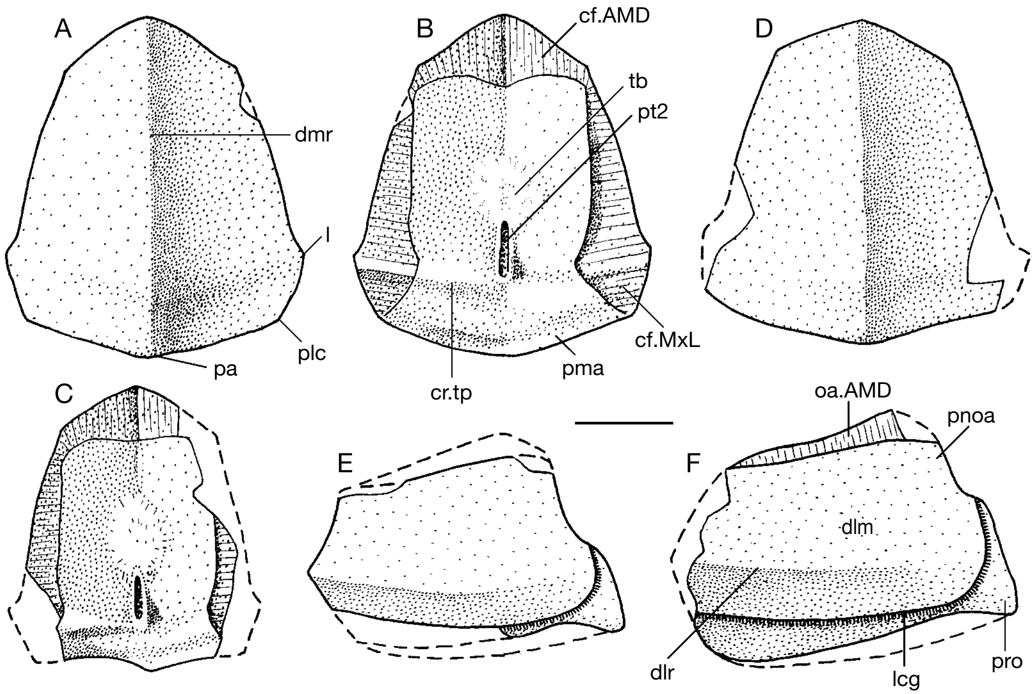

FIG. 58. — *Bothriolepis jani* Lukševičs, 1986; **A**-**D**, PMD; **A**, **B**, LDM 100/83 in dorsal and visceral views; **C**, LDM 100/84 in visceral view; **D**, LDM 100/80 in dorsal view; **E**, **F**, ADL; **E**, LDM 100/121; **F**, LDM 100/122. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **cf.AMD**, area overlapping AMD; **cf.MxL**, area overlapping MxL; **cr.tp**, crista transversalis interna posterior; **dlm**, dorsal lamina; **dlr**, dorso-lateral ridge; **dmr**, dorsal median ridge; **l**, lateral corner of PMD; **lcg**, main lateral line groove; **oa.AMD**, area overlapped by AMD; **pa**, posterior corner; **plc**, postero-lateral corner; **pma**, posterior marginal area; **pnoa**, postnuchal ornamented corner; **pro**, processus obstans; **pt2**, posterior ventral pit; **tb**, ventral tuberosity. Scale bar: 5 mm.

developed, it can be recognised only in LDM 100/372 (Fig. 56G) as a sharp transversely directed crest binding the orbital facets posteriorly.

The dorsal trunk armour is relatively broad, B/L index 90. It is relatively low, with a lateral wall less than three times as long as high, with high dorsal wall. Length of the dorsal wall reaches 65 mm. Right and left dorsal laminae enclose an angle about 115°. The dorsal and lateral walls enclose an angle 120° in the MxL and about 125-130° in the ADL. The median dorsal ridge is well-defined. The dorso-lateral and ventro-lateral ridges are well-marked in a posterior part of the trunk armour.

The AMD (Figs 55J-L; 57) with B/L index about 91-110, 97 on the average, in large individuals it is broader than long, as in *B. maxima*. The plate is strongly arched, with right and left laminae forming an angle at the level of lateral corners of about 115° on the average. The anterior margin may be weakly concave or fairly straight. It is broad and 1.2-2 times as long as a narrow posterior margin. The tergal angle (dma) is well-marked. The median dorsal ridge is strongly developed and in small individuals represented by the low crest. Overlap areas for MxL are developed as in *Remigolepis* (Stensiö 1931). The visceral surface of the AMD shows a broad levator fossa (f.retr), which is limited by the low postlevator thickenings (alr) and strongly developed postlevator crest (cr.pl) with pronounced kink. The anterior edge of the crest do not reach a distinct, but narrow supranuchal area.

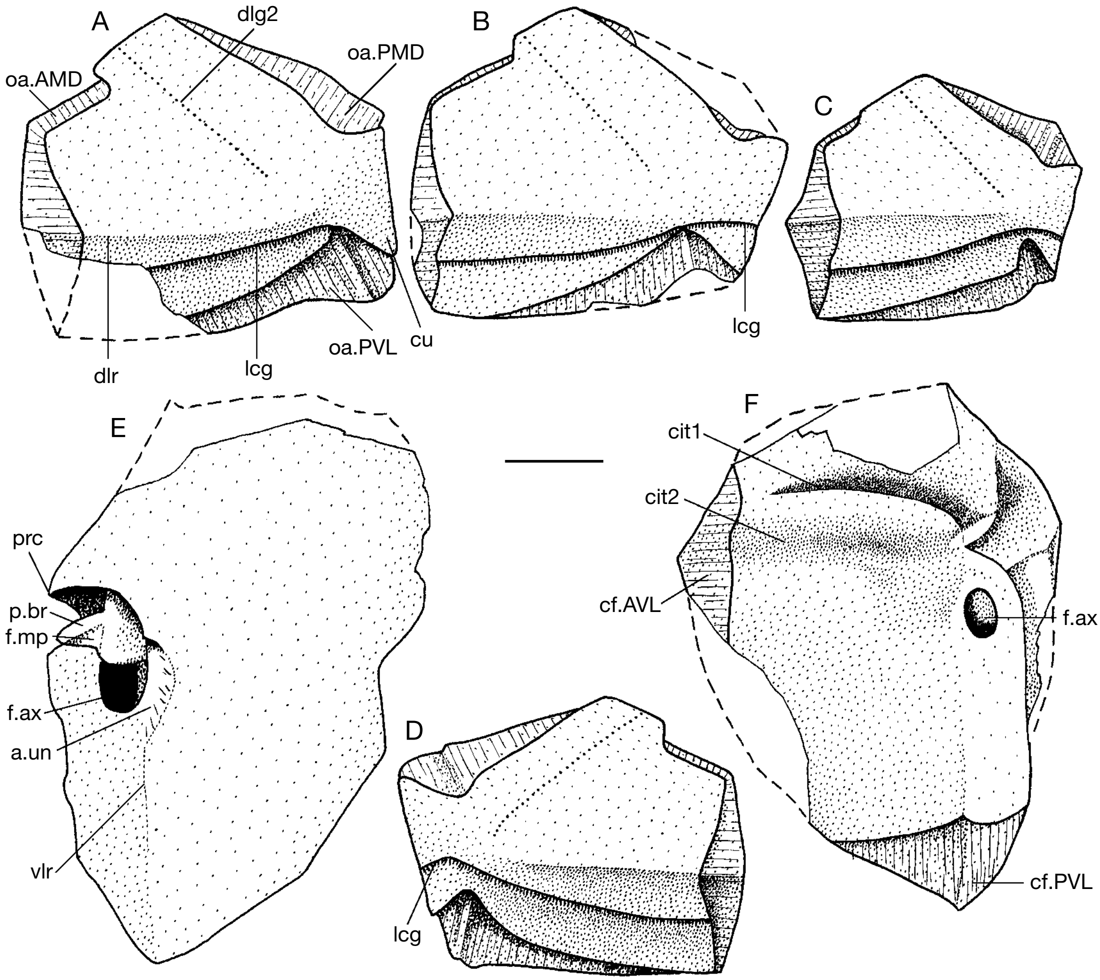

FIG. 59. — *Bothriolepis jani* Lukševičs, 1986; **A**-**D**, MxL in dorsal view; **A**, LDM 100/87; **B**, LDM 100/90; **C**, LDM 100/432; **D**, holotype LDM 100/88; **E**, **F**, AVL; **E**, LDM 100/433 in ventral view; **F**, LDM 100/102 in visceral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **MxL**, mixilateral plate; **PVL**, posterior ventro lateral plate; **a.un**, unornamented area beneath fossa articularis pectoralis; **cf.AVL**, area overlapping AVL; **cf.PVL**, area overlapping PVL; **cit1**, crista transversalis interna anterior; **cit2**, transverse thickening; **cu**, postero-ventral ornamented corner; **dlg2**, posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge; **f.ax**, axillary foramen; **f.mp**, protractor area of processus brachialis; **La**, lateral plate; **lcg**, main lateral line groove; **oa.AMD**, area overlapped by AMD; **oa.PMD**, area overlapped by PMD; **oa.PVL**, area overlapped by PVL; **p.br**, processus brachialis; **prc**, prepectoral corner; **vlr**, ventro-lateral ridge. Scale bar: 5 mm.

The PMD (Figs 55H-I; 58A-D) is arched, moderately broad, B/L index about 87-104. The width of the anterior margin comprises about 54% of total breadth. The median dorsal ridge is well-developed.

The ADL (Figs 55M, N; 58E, F) is moderately broad. The dorsal lamina is relatively narrow and long, and its breadth a little exceeds height of the lateral lamina. Dorsal and lateral laminae of the plate enclosing an angle of 125-130°. The dorso-lateral ridge (dlr) is well-defined in the posterior part of the plate, it is rounded in the anterior third of the ADL.

The dorsal lamina of the MxL (Figs 55O-R; 59A-D) is less than twice as long as it is broad.

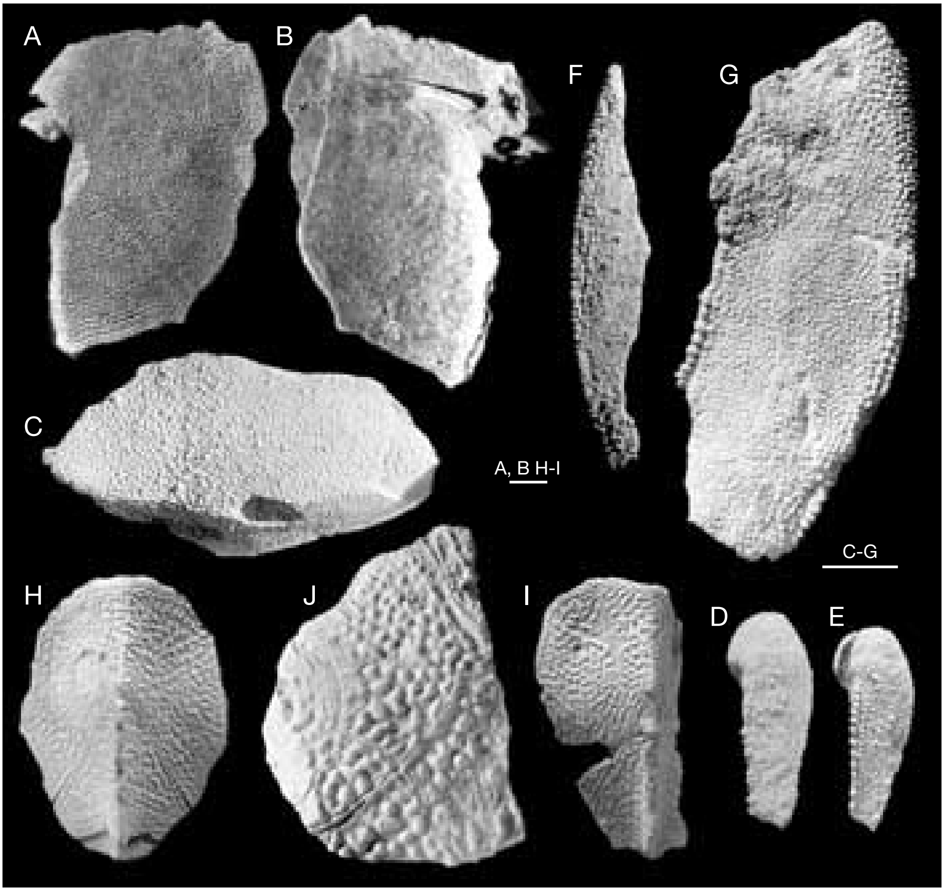

FIG. 60. — **A**-**G**, *Bothriolepis jani* Lukševičs, 1986; **A**, **B**, AVL LDM 100/98 in ventral and visceral views; **C**, PVL LDM 100/434; **D**, CD1 plate LDM 100/144; **E**, CD1 LDM 100/436; **F**, ML2 LDM 100/378; **G**, proximal segment of the pectoral fin LDM 100/435. Skujaine River near Klūnas village, Latvia. Tērvete Formation; **H**-**J**, *Bothriolepis heckeri* n. sp.; **H**, holotype, AMD plate PIN 835/42 in dorsal view; **I**, incomplete AMD plate PIN 835/41 in dorsal view; **J**, incomplete La, Pn and Pmg PIN 835/40 in dorsal view. Malyi Tuder River not far from Bilovo village, Russia. Bilovo Beds(?). Abbreviations: **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD1**, central dorsal plate 1; **ML2**, lateral marginal plate 2; **PVL**, posterior ventro lateral plate; **La**, lateral plate; **Pn**, paranuchal plate; **Pmg**, postmarginal plate. Scale bars: 5 mm.

The dorsal lamina is 1.7 time as broad as the lateral lamina is high. Dorsal and lateral laminae enclosing an angle about 120°. The lateral lamina is relatively high, 2.4 times as long as it is broad. The dorso-lateral ridge is well-defined. The lateral line sensory groove terminates on the posterior margin of the plate above the postero-ventral ornamented corner (cu), posterior part of the sensory groove is traced not along the suture between the MxL and PMD as usually in *Bothriolepis*, but on the outer surface of the MxL.

The AVL (Figs 59E, F; 60A, B) is of moderate breadth, the ventral lamina is about 2.5 times as long as it is broad. The ventral lamina 2.3 times as broad as the lateral lamina high in LDM 100/433 (Fig. 59E). Ventro-lateral ridge is well-defined. The axillary foramen (f.ax) is rather large and slightly elongated in shape. The visceral surface of the AVL shows the high transverse anterior crista (cit1) running mesially subparallel to the low and broad transverse thickening (cit2), just like as in *B. ciecere*, *B. macphersoni* Young, 1888 and *B. karawaka* Young, 1888.

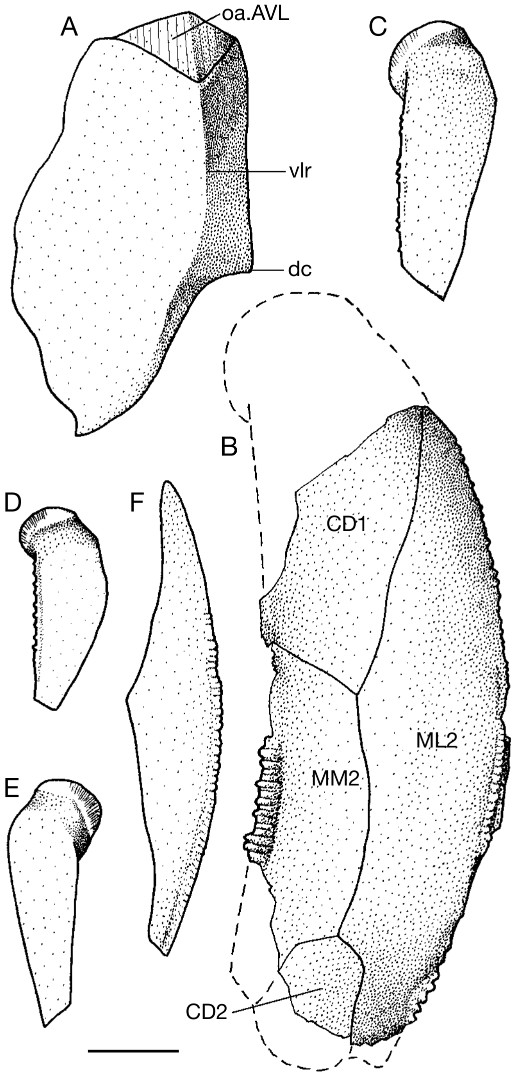

FIG. 61. — *Bothriolepis jani* Lukševičs, 1986; **A**, PVL LDM 100/434; **B**, proximal segment of the pectoral appendage LDM 100/435; **C**, CD1 LDM 100/130; **D**, CD1 LDM 100/133; **E**, CV1 LDM 100/134; **F**, ML2 LDM 100/378. Skujaine River near Klūnas village, Latvia. Tērvete Formation. Abbreviations: **CD1**, **2**, central dorsal plates 1 and 2; **CV1**, ventral central plate 1; **ML2**, lateral marginal plate 2; **MM2**, mesial marginal plate 2; **dc**, dorsal corner of lateral lamina; **oa.AVL**, area overlapped by AVL; **PVL**, posterior ventro lateral plate; **vlr**, ventro-lateral ridge. Scale bar: 5 mm.

There are two complete PVL LDM 100/434 (Figs 60C; 61A) and LDM 100/375. In LDM 100/434, its ventral lamina is 2.1 times as long as it is broad. The subanal division is relatively broad, it occupies only 17.7% of the total PVL length. The lateral lamina is 2.6 times as long as it is high, the ventral lamina is 1.5 time as broad as the lateral lamina high. The ventral and lateral laminae encloses the angle about 112°. The ventro-lateral ridge (vlr) is well-developed.

The MV is unknown, but the shape of the AVL and PVL suggests the small size of the MV.

The pectoral fin is represented mostly by disarticulated bones, and specimen LDM 100/435 (Figs 60G; 61B) showing articulated plates of the proximal segment without the most proximal part. The proximal segment bears large prominent lateral and mesial spines. It is relatively broad, about three times as long as it is broad. The CD1 is of moderate size with L/B index varying from 2.8 to 3. The CV1 is slightly more elongated than the CD1 (L/B 3.3). The ML2 is 4.4-5.5 (4.9 on the average) as long as it is broad.

The ornamentation is reticulate in small individuals and typically tuberculate in well-grown individuals. It consists of numerous closely and usually irregularly set tubercles, which usually are rounded. They are tall on the Prm and short on most of the other plates. Along the obtected nuchal area on the Nu and posterior margin of the lateral lamina of the PVL tubercles may fuse into ridges. More regular setting of tubercles is recognized on the proximal segment of the pectoral fin.

REMARKS

The holotype and most of the material (collection LDM 100) came from the Skujaine locality, collected by the author in 1984, 1989 and 1998. Some studied specimens (e.g., LGI 5/2028) were found by Karatajūte-Talimaa in the same locality. Other material (e.g., LDM 100/524) was collected by the author in the Ķurbes locality.

DISCUSSION

B. jani differs from most of other *Bothriolepis* by its tuberculate ornament, which is similar to that of *Grossilepis tuberculata* and *G. spinosa*.

B. jani differs from *G. tuberculata* in its 1) shape and proportions of the PMD, MxL and PVL; 2) sutural connections of the AMD and MxL; 3) shape of the postnuchal ornamented corner of the ADL; 4) larger axillary foramen; 5) proportions of pectoral fin bones.

Most of the described specimens come from the locality at Skujaine River downstream Klūnas village, associated with *B. ornata*. A comparison of *B. jani* with *B. ornata* is given at the end of the description of *B. ornata*.

B. jani can be distinguished readily from the other Famennian *Bothriolepis* species of similar size (*B. cristata*, *B. hydrophila* [Miles 1968] and small specimens of *B. ciecere*) by its tuberculate ornament. *B. jani* differs well from *B. nielseni* Stensiö, 1948 in absence of the crest on the dorso-lateral ridge. *Bothriolepis*, described by Gross (1942) from locality at Svēte River, resembles *B. jani* by its tubercular ornament but differs in absence of a prominent ventro-lateral ridge on the PVL. The species *B. jani* and *B. lohesti* Leriche, 1931 (see Stensiö 1948) from Belgium are similar in 1) the shape and proportions of the AMD; 2) sutural connections between AMD and MxL. Unfortunately, *B. lohesti* is only represented by a few remains of AMD, ADL and pieces of the pectoral fin bones. It differs in that 1) the AMD is less arched; 2) ornament consists of tubercles and nodose ridges, but it seems likely that *B. jani* and *B. lohesti* may be phylogenetically very close.

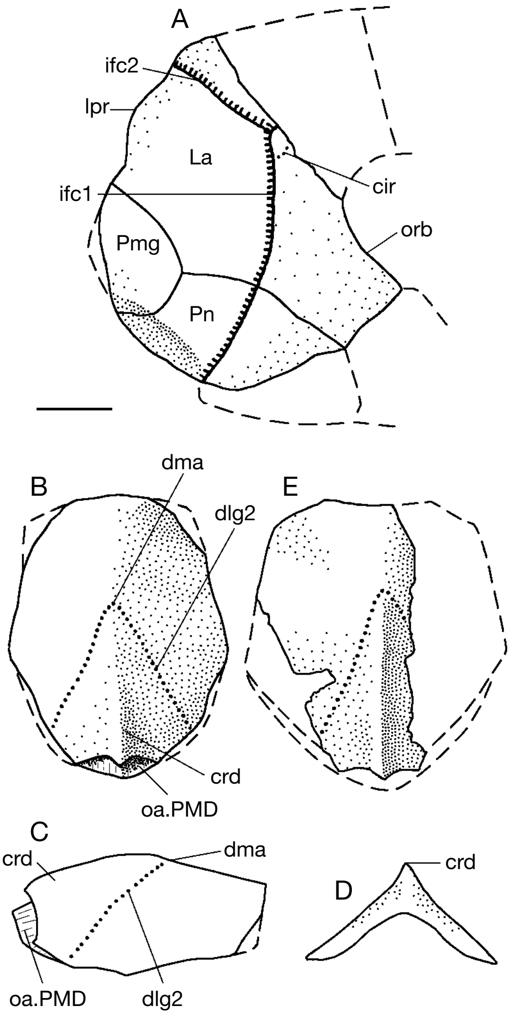

FIG. 62. — *Bothriolepis heckeri* n. sp.; **A**, incomplete La, Pn and Pmg PIN 835/40; **B**-**D**, holotype, AMD PIN 835/42; **B**, dorsal view; **C**, lateral view; **D**, anterior view; **E**, incomplete AMD PIN 835/41 in dorsal view. Malyi Tuder River not far from Bilovo village, Novgorod region, Russia. Bilovo Beds(?). Abbreviations: **AMD**, anterior median dorsal plate; **PMD**, posterior median dorsal plate; **La**, lateral plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **cir**, semicircular pit-line groove; **crd**, dorsal median crista; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **lpr**, lateral process; **oa.PMD**, area overlapped by PMD; **orb**, orbital margin. Scale bar: 10 mm.

Bothriolepis heckeri n. sp.
(Figs 60H-J; 62)

HOLOTYPE. — AMD PIN 835/42.

MATERIAL EXAMINED. — PIN 835/41, an incomplete AMD; PIN 835/40, an incomplete La, Pn and Pmg; all gathered by R. Hecker in 1930.

LOCALITY AND HORIZON. — Outcrop at the right bank of Malyi Tuder River not far from Bilovo village, Novgorod region, Russia; Bilovo Beds(?), Famennian.

DIAGNOSIS. — Moderately large *Bothriolepis* with comparatively narrow and strongly arched AMD (B/L index of about 81) which bears high dorsal median crest arising just anteriorly the tergal angle. La is broad with very long infraorbital sensory groove diverging on La.

Description

PIN 835/42 is a relatively small almost complete AMD with damaged antero-lateral corners (Figs 60H; 62B-D) and PIN 835/41 is an imperfect AMD without the right lateral margin and loosed left postero-lateral margin (Figs 60I; 62E). The AMD is comparatively narrow with B/L index of about 81, with a gently concave anterior margin, which is moderately broad. The posterior margin is relatively narrow, about 1.2 time shorter than the anterior margin. The AMD is strongly arched with the angle between the two laminae about 100°, and bears a 2-3 mm high dorsal median crest (cr.d) which arises just anteriorly the tergal angle. The antero-lateral corner is weakly defined. The tergal angle is situated slightly posteriorly the anterior third of the plate. The posterior oblique dorsal sensory line grooves (dlg2) are well-defined. The ornament is reticular, sometimes with slightly defined ridges.

PIN 835/40 is an incomplete head-shield consisting of the Pn, Pmg and incomplete La which lacks the margin making contact with the Prm (Figs 60J; 62A). The La plate is relatively broad as it is preserved, with gently defined antero-lateral corner. The infraorbital sensory groove crosses the plate far from the lateral and rostral margins. The central sensory line groove (csl) seem to finish at the level of the middle of an orbital fenestra length. The branch of the infraorbital sensory groove diverging on La (ifc2) is well-defined and unusually long. The Pn seems to be relatively broad as it is preserved. The Pmg of unusual shape with the median margins longer than the lateral margins.

Discussion

Bothriolepis heckeri n. sp. differs from all the other known *Bothriolepis* from the Main Devonian Field in its broad La with unusually situated sensory grooves. *B. cristata* (Miles 1968) from the Rosebrae Beds of Scotland also has a strongly developed dorsal median crest, but differs in other shape and general proportions of the AMD.

Bothriolepis ciecere Lyarskaja *in* Lyarskaja & Savvaitova, 1974 (Figs 63-76)

Bothriolepis ciecere Lyarskaja in Lyarskaja & Savvaitova, 1974: 99-104, pl. I, fig. 1.

Bothriolepis ornata Eichw. – Gross 1933: 41.

Bothriolepis cf. *ornata* Eichw. – Gross 1942: 421-422, abb. 2. — Lyarskaja & Savvaitova 1974: 97.

Bothriolepis pavariensis – Lyarskaja & Savvaitova 1974: 104, pl. I, figs 5-7; text-figs 9-10.

Holotype. — AMD LDM 43/303.

Material examined. — LDM 43/301, 43/303-306, 43/337, 43/5082, 43/5095, 43/5120, 57/1-97, 57/398, 57/721, 57/722, 57/724-726, 57/728-733, 57/896, 57/906, 57A/1, 81/1-41, 81/43-46, 81/48-94, 81/96-98, 81/126, 81/127, 81/136-155, 81/157-164, 81/170-183, 81/190-275, 81/279-351, 81/356-358, 81/360-363, 81/365-377, 81/380-393, 81/406-504, 81/533-549, 81/554-556, 81/558-577, LGI 5/2020 - 5/2044): articulated head-shields and their fragments, disarticulated plates of the head-shield, trunk-armour and pectoral appendage.

Localities and horizon. — The type locality is an outcrop at the left bank of Ciecere River downstream from the Pavāri hamlet; upper Famennian, the middle Member of the Ketleri Formation. Other material comes from an outcrop exposing light sand and sandstone at the right bank of Venta River 1 km W from Ketleri hamlet; the upper Member of the Ketleri Formation. A probable other undescribed subspecies of B. ciecere comes from Rybnitsa quarry, Oryol region of Russia; Turgenevo Beds of the Plavsk Regional Stage, Famennian (Lebedev 1995; Lebedev & Lukševičs 1996).

Diagnosis. — Rather large *Bothriolepis* with a median dorsal armour length of at least 200 mm. Dorsal wall of moderate width, B/L index of trunk-armour about 77. B/L index of the head-shield of 120. Preorbital recess of trifid type. Orbital edges of Prm and La thickened. Anterior margin of the head-shield is rounded. Orbital fenestra is not large. Prm broad, posterior margin is slightly shorter than anterior margin. Nu strongly vaulted, moderately broad, L/B index of 80. AMD moderately broad, B/L index 87. Posterior margin of AMD and anterior margin of PMD are very narrow. Median dorsal ridge poorly developed. Dorsolateral ridge well-marked, bears smooth tubercles. Ventrolateral ridge strongly developed forming a well-defined crest in a posterior part of armour. Ornamentation typically reticulate, in quite large individuals becoming coarser and sparser.

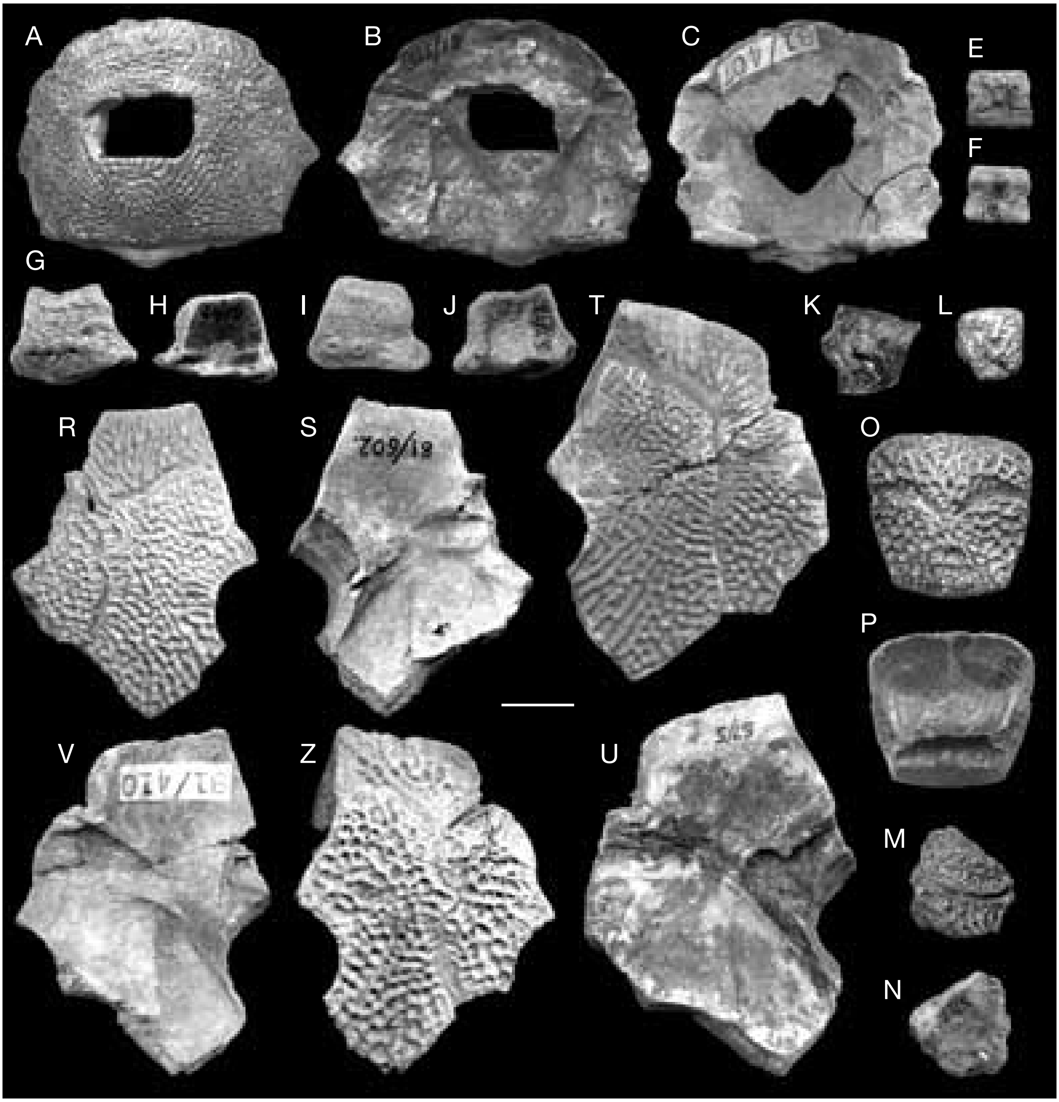

FIG. 63. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**-**C**, head-shields in dorsal (**A**) and visceral (**B**, **C**) views; **A**, **B**, LDM 81/545; **C**, LDM 81/407; **E**-**J**, Pi in dorsal (**E**, **G**, **I**) and visceral (**F**, **H**, **J**) views; **E**, **F**, LDM 57/10; **G**, **H**, LDM 57/13; **I**, **J**, LDM 57/12; **K**-**N**, Prl in dorsal (**K**-**M**) and visceral (**N**) views; **K**, LDM 57/732; **L**, LDM 57/910; **M**, **N**, LDM 57/7; **O**, **P**, Prm LDM 57/2 in dorsal and visceral views; **R**-**Z**, La in dorsal (**R**, **T**, **Z**) and visceral (**S**, **U**, **V**) views; **R**, **S**, LDM 81/602; **T**, **U**, LDM 57/5; **V**, **Z**, LDM 81/410. A-C, R, S, V, Z, Ciecere River near Pavāri hamlet, Latvia; E-P, T, U, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviations: **La**, lateral plate; **Pi**, pineal plate; **Prl**, prelateral plate; **Prm**, premedian plate. Scale bar: 10 mm.

DESCRIPTION

The head-shield (Figs 63A-C; 65A, B) was not described by Lyarskaja (Lyarskaja & Savvaitova 1974). It is strongly vaulted both rostrocaudally and transversely. The rostral margin is strongly convex, much shorter than the posterior margin, which is weakly convex. There are well-defined anterolateral corners (alc) and the deep prelateral notch (nprl). The obtected nuchal area (nm) is short, broadest on the Nu, with slightly defined lateral and median processes. The orbital fenestra is relatively small, with a B/L index about

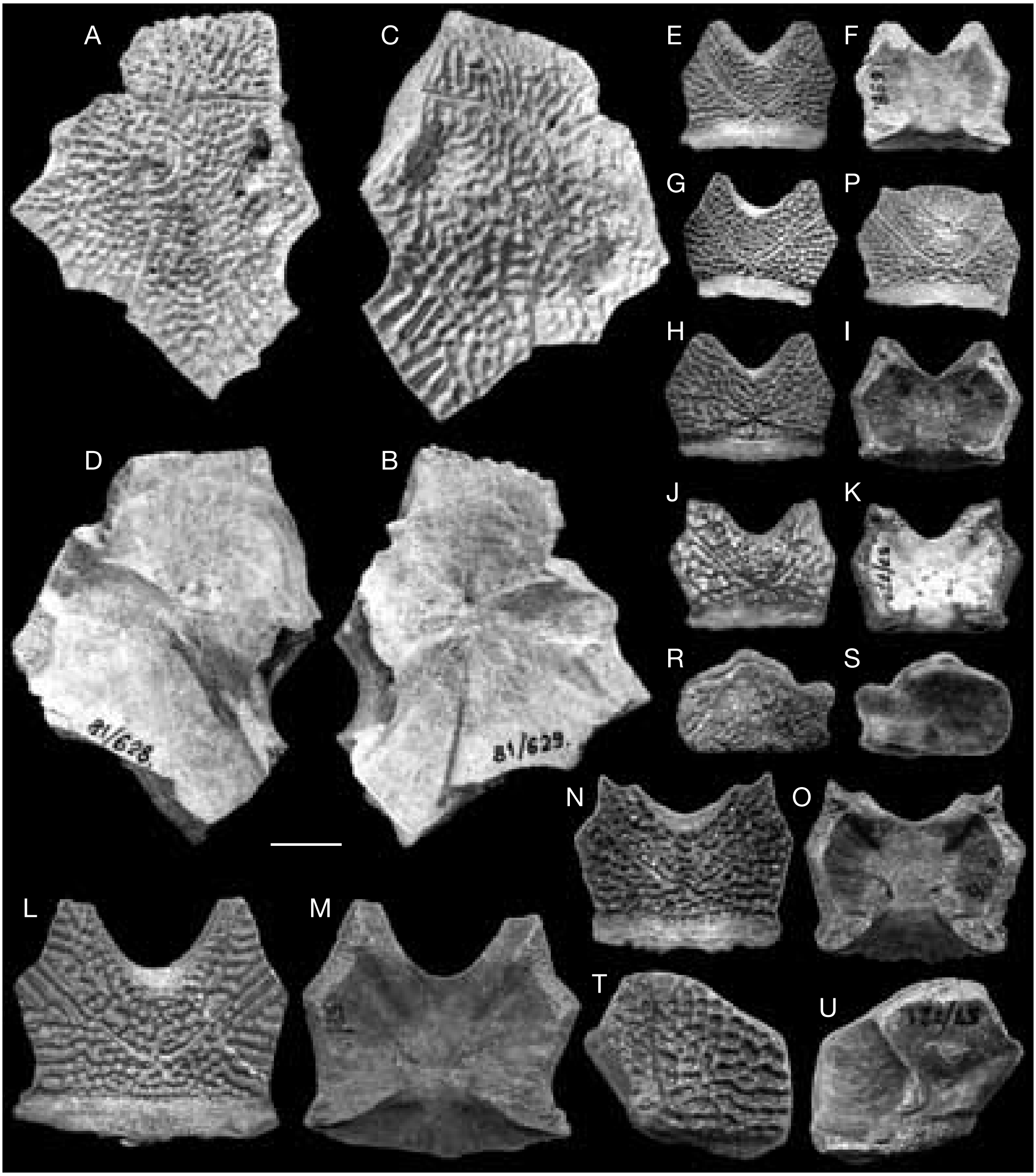

FIG. 64. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**-**D**, La in dorsal (**A**, **C**) and visceral (**B**, **D**) views; **A**, **B**, LDM 81/629; **C**, **D**, LDM 81/628; **E**-**O**, Nu in dorsal (**E**, **G**, **H**, **J**, **L**, **N**) and visceral (**F**, **I**, **K**, **M**, **O**) views; **E**, **F**, LDM 81/698; **G**, LDM 81/811; **H**, **I**, LDM 57/14; **J**, **K**, LDM 57/723; **L**, **M**, LDM 57/18; **N**, **O**, LDM 57/909; **P**, articulated Nu and Pp 81/412 in dorsal view; **R**, **S**, Sm LDM 57/328 in dorsal and visceral views; **T**, **U**, Pn 57/721 in dorsal and visceral views. A-G, P, Ciecere River near Pavāri hamlet, Latvia. H-O, R-U, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Sm**, submarginal plate. Scale bar: 10 mm.

190 (n = 6). The orbital edges of the Prm and La are thickened, similarly as in *B. ornata*, *B. macphersoni* and *B. karawaka*.

The visceral skull surface (Fig. 63B, C) shows the broad otico-occipital depression (ood), which is well-defined by the paramarginal cristae

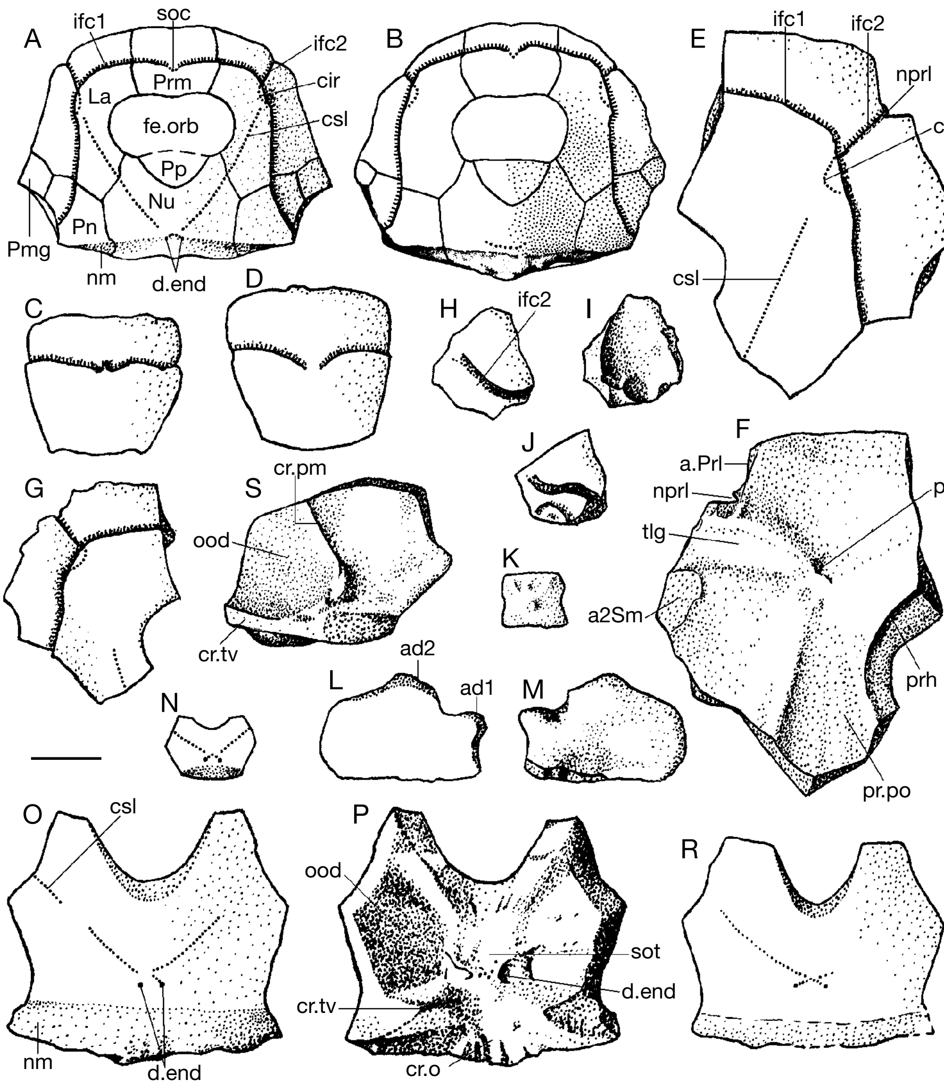

FIG. 65. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**, **B**, head-shields in dorsal view; **A**, LDM 81/25; **B**, LDM 81/545; **C**, **D**, Prm; **C**, LGI 5/2034; **D**, LDM 57/2; **E**-**G**, La; **E**, **F**, LDM 57/5 in dorsal and visceral views; **G**, LGI 5/2044; **H**-**J**, left-side Prl; **H**, **I**, LDM 57/7 in dorsal and visceral views; **J**, LDM 57/732 in dorsal view; **K**, Pi LDM 57/10; **L**, **M**, Sm LDM 57/328 in dorsal and visceral views; **N**-**R**, Nu in dorsal (**N**, **O**, **R**) and visceral (**P**) views; **N**, LGI 5/2029; **O**, **P**, LDM 57/18; **R**, LGI 5/2025; **S**, Pn LDM 57/721 in visceral view. A, B, Ciecere River near Pavāri hamlet, Latvia. C-S, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prl**, prelateral plate ; **Prm**, premedian plate; **Sm**, submarginal plate; **ad1**, **2**, anterior and posterior articular processes; **a.Prl**, attachment area for Prl; **a2Sm**, posterior attachment area for Sm; **cir**, semicircular pit-line groove; **cr.o**, median occipital crista; **cr.pm**, paramarginal crista; **cr.tv**, transverse nuchal crista; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **fe.orb**, orbital fenestra; **ifc1**, principal section of infraorbital sensory line; **ifc2**, branch of infraorbital sensory line diverging on La; **nm**, obtected nuchal area; **nprl**, prelateral notch; **ood**, otico-occipital depression; **p**, lateral pit of head-shield; **prh**, preorbital recess; **pr.po**, antero-lateral corner of otico-occipital depression; **soc**, anterior section of the supraorbital sensory line; **sot**, supraotic thickening; **tlg**, transverse lateral groove. Scale bar: 10 mm.

(cr.pm). The antero-lateral corner of otico-occipital depression (pr.po) is broad in its base, postero-lateral corner is rounded and extends laterally over the middle of the Pn's posterior margin. The transverse lateral groove (tlg) is moderately broad and clearly defined. A broad

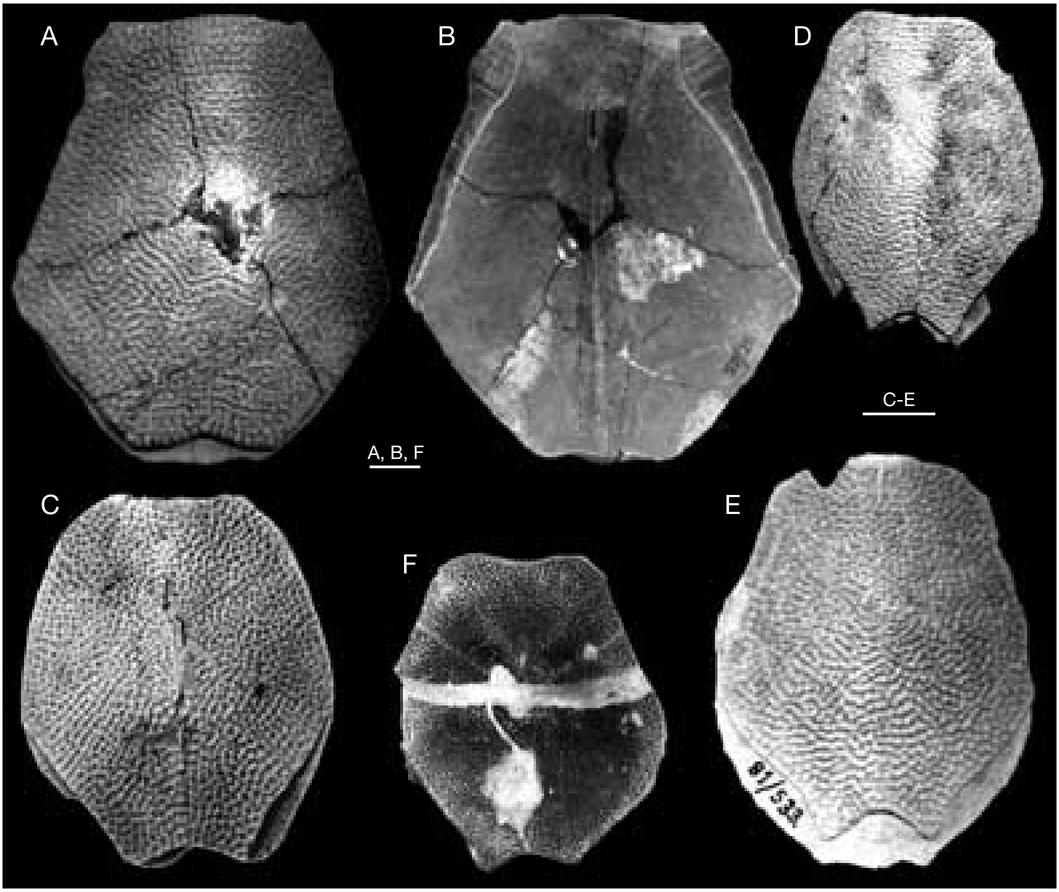

FIG. 66. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, AMD in dorsal (**A**, **C**-**F**) and visceral (**B**) views; **A**, **B**, LDM 57/25; **C**, holotype LDM 43/303; **D**, LDM 81/725; **E**, LDM 81/533; **F**, LDM 81/372. C-F, Ciecere River near Pavāri hamlet, Latvia. A, B, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviation: **AMD**, anterior median dorsal plate. Scale bars: 10 mm.

shallow depression anteriorly from the antero-lateral corner of preorbital recess is the lateral pit (p), which is situated equally spaced from an orbital edge of La and prelateral notch. The lateral margin shows very broad attachment areas for the Sm with the strikingly short posterior one (a.2Sm). The attachment area for the Prl is almost laterally rather then ventrally faced. The median occipital crista (cr.o) is slightly defined, often it consists of several radially situated small ridges.

The Prm (Figs 63O, P; 65C, D) with B/L index 94-118. A rostral angle (ac) is present in half of large individuals. The orbital margin bears gently defined nasal notch (pnn). The anterior section of the supraorbital sensory line (soc) is observed not always. There are several tubercles and pits of various shape and size usually situated on the dorsal surface of the preorbital recess.

The La (Figs 63O, P; 64A-D; 65E-G) is moderately broad with the L/B index 136 on the average. The rostral margin is of moderate breadth and almost straight, the antero-median and antero-lateral corners are well-defined.

The Pi (Figs 63E-J; 65K) was for the first time described by Lukševičs (1991), it is known only from the Ketleri locality. Pi is relatively broad, breadth slightly exceeds a length. There is a

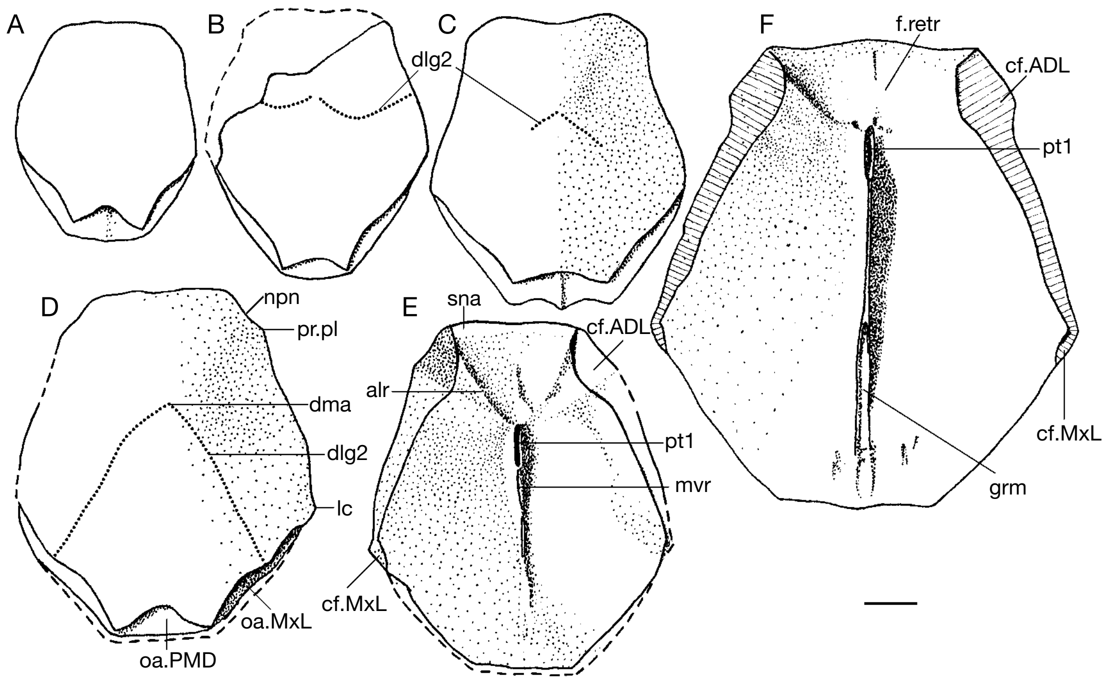

FIG. 67. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, AMD in dorsal (**A**-**D**) and visceral (**E**, **F**) views; **A**, LDM 81/251; **B**, LDM 81/36; **C**, LDM 81/28; **D**, **E**, LGI 5/2020; **F**, LDM 57/25. A-C, Ciecere River near Pavāri hamlet, Latvia. D-F, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **alr**, postlevator thickening; **cf.ADL**, area overlapping ADL; **cf.MxL**, area overlapping MxL; **dlg2**, posterior oblique dorsal sensory line groove; **dma**, tergal angle; **f.retr**, levator fossa; **grm**, ventral median groove; **lc**, lateral corner; **mvr**, median ventral ridge; **npn**, postnuchal notch; **oa.MxL**, area overlapped by MxL; **oa.PMD**, area overlapped by PMD; **pr.pl**, external postlevator process; **pt1**, anterior ventral pit; **sna**, supranuchal area. Scale bar: 10 mm.

broad area without ornamentation along the posterior margin. A deep, but small pineal pit and antero-laterally situated paired tubercles are present on the visceral surface of the plate. Position of the pineal pit is marked on the outer surface by the pineal elevation or pineal fenestra.
The Nu (Figs 64E-O; 65N-R) is vaulted (Lyarskaja & Savvaitova 1974) with an angle between right and left halves slightly larger than 130°, L/B index 68-93, 80 on the average. The anterior division of the lateral margin is concave even in very large specimen, but not straight, as was shown by Lyarskaja for *B. pavariensis* (Lyarskaja & Savvaitova 1974: fig. 9), and a little shorter than the posterior division. The shape of the posterior margin is variable, however it always bears the posterior process (mppr). The central sensory line groove is clearly distinct in small individuals, in well-grown specimens sometimes it is present only on one side of the plate (LGI 5/2025: Fig. 65R), interrupted or very short (LDM 57/14: Fig. 64H; LDM 57/18: Fig. 64L; LDM 57/723: Fig. 64J). In some cases there are short supraoccipital grooves, which terminate little in front of the obtected nuchal area at the rather large external openings for the endolymphatic ducts (d.end). Postorbital crista on the visceral surface is low.
The Pn is of moderate breadth, L/B index 88-110. The lateral division of the Pn is relatively narrow composing 40-50% of the general breadth of a plate. The Pmg is relatively broad with lateral margins slightly longer than the median margins (Lyarskaja & Savvaitova 1974).
The single Sm (extralateral) (Figs 64R, S; 65L, M), collected by Lukševičs (LDM 57/328) is relatively

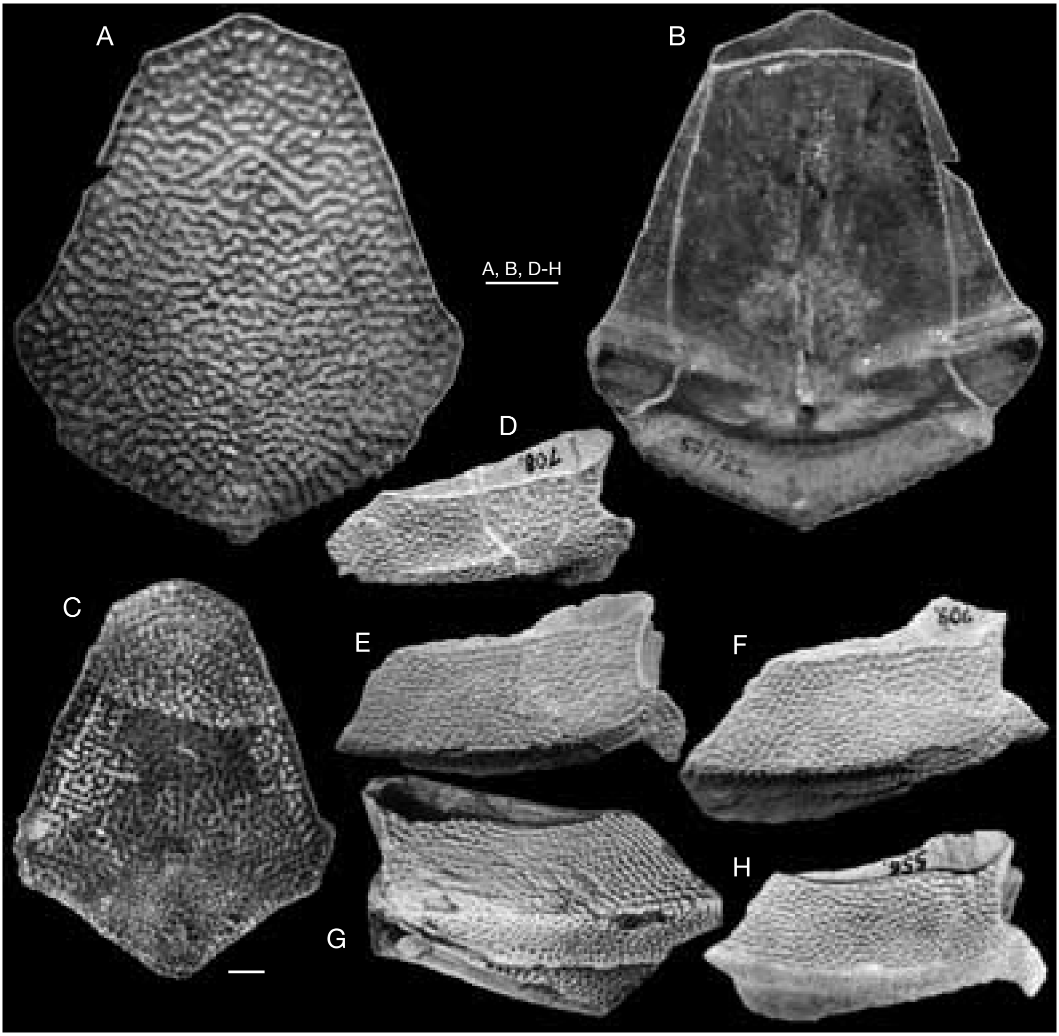

FIG. 68. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, PMD; **A**, **B**, LDM 57/722 in dorsal and visceral views; **C**, LGI 5/2023, in dorsal view; **D**-**H**, ADL in dorsal view; **D**, LDM 81/708; **E**, LDM 43/306; **F**, LDM 81/709; **G**, LDM 81/371; **H**, LDM 81/556. D-H, Ciecere River near Pavāri hamlet, Latvia. A-C, Venta River near Ketleri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **PMD**, posterior median dorsal plate. Scale bars: 10 mm.

short with a L/B index about 150. The dorsal margin has a prominent anterodorsal process and posterior attachment area for the skull. The posterior margin is strongly convex, the ventral margin is weakly concave.

The trunk-armour in individuals of moderate size is known from many isolated plates, partial dorsal wall of the trunk-shield prepared from visceral surface consisting of AMD, PMD, left ADL and MxL (LDM 81/58-81/60), and several articulated bones. Plasticine reconstruction was used to describe the features of the trunk-armour.

The trunk-armour was not described by Lyarskaja (Lyarskaja & Savvaitova 1974) in details. In individuals of moderate size it is relatively broad (B/L index 77), low, with a lateral wall less than three times as long as it is high; in

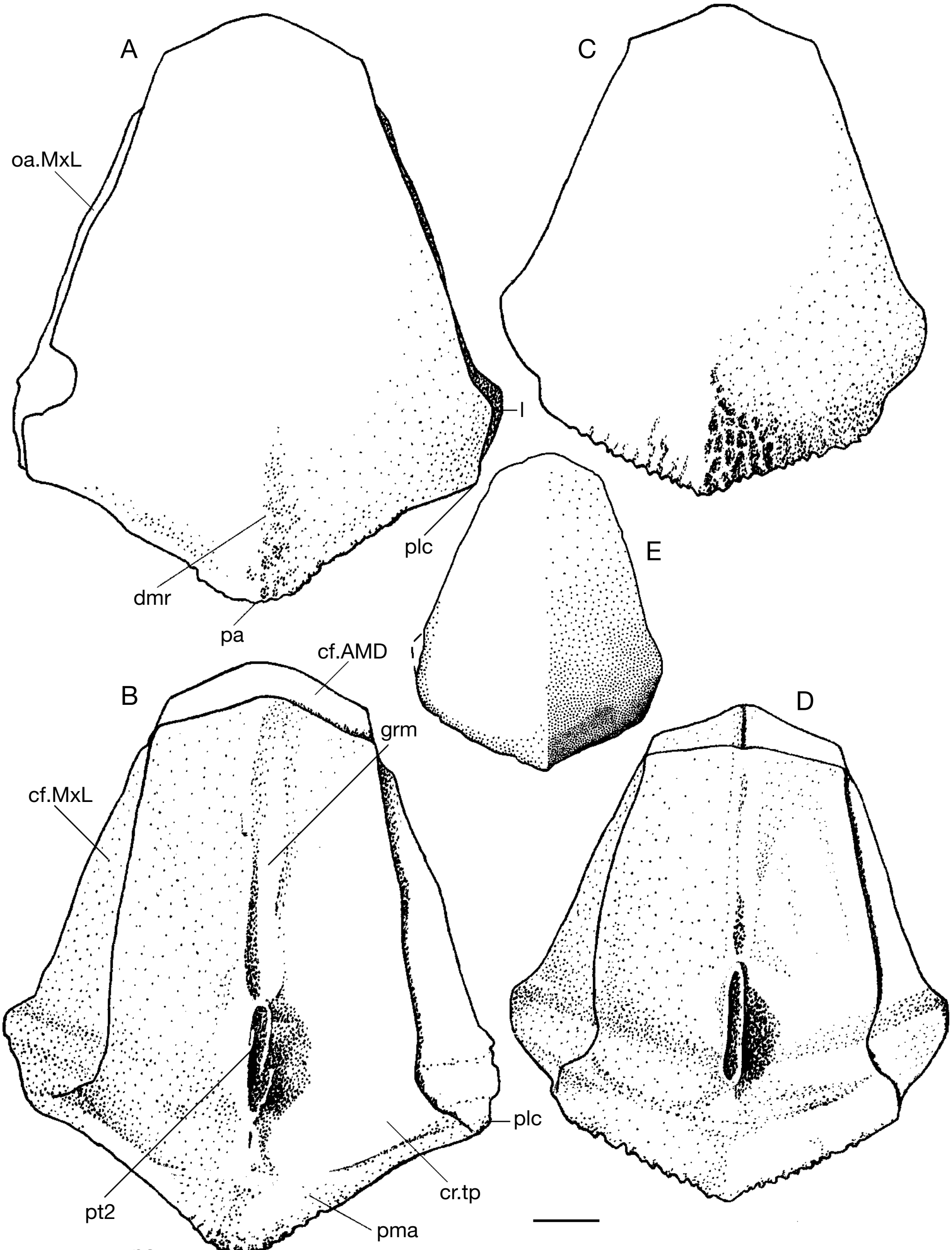

FIG. 69. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, PMD; **A**, **B**, LGI 5/2023 in dorsal and visceral views; **C**, **D**, LDM 57/722, in dorsal and visceral views; **E**, 81/704 in dorsal view. A-D, Venta River near Ketleri hamlet, Latvia. E, Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **AMD**, anterior median dorsal plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **cf.AMD**, area overlapping AMD; **cf.MxL**, area overlapping MxL; **cr.tp**, crista transversalis interna posterior; **dmr**, dorsal median ridge; **grm**, ventral median groove; **l**, lateral corner; **oa.MxL**, area overlapped by MxL; **pa**, posterior corner; **plc**, postero-lateral corner; **pma**, posterior marginal area; **pt2**, posterior ventral pit. Scale bar: 10 mm.

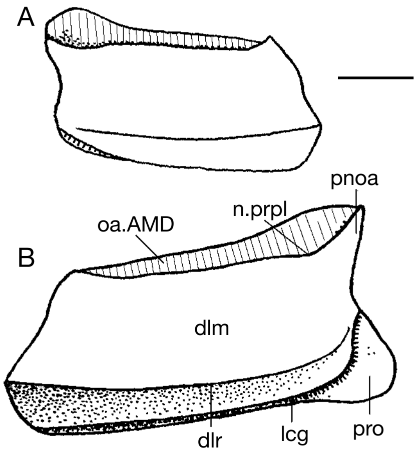

FIG. 70. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, ADL; **A**, LDM 81/62; **B**, LDM 81/245. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **dlm**, dorsal lamina; dlr, dorso-lateral ridge; **lcg**, main lateral line groove; **n.prpl**, notch in dorsal margin of ADL for external postlevator process of AMD; **oa.AMD**, area overlapped by AMD; **pnoa**, postnuchal ornamented corner; **pro**, processus obstans. Scale bar: 10 mm.

comparison with some other species rather flattened with low dorsal wall. The length of the dorsal wall, probably, reaches more than 200 mm. The ventral wall is not quite flat, but slightly vailted transversely. It is gently arched also in rostrocaudal direction in the posterior division of the armour. The median dorsal ridge is weakly defined, it is present only in the posterior quarter of the PMD. The dorso-lateral and ventro-lateral ridges are well-marked, strongly developed in a posterior part of the armour forming a well-defined crests. Both ridges bear a row of numerous, closely set smooth tubercles, which gradually increase in caudal direction. This feature distinguishes *B. ciecere* from all the other known *Bothriolepis* from the Baltics, resembling *B. nielseni* from Greenland (Stensiö 1948: text-fig. 308).

The AMD (Figs 66; 67) is moderately broad, B/L index about 76-98, 87 on the average. The anterior part of the plate is arched, with right and left laminae forming an angle at the level of lateral corners of about 139°, posterior part is more flattened. The anterior margin is weakly concave or less often fairly straight (in large individuals), moderately broad and 1.1-1.7 time as long as a narrow posterior margin. Overlap areas for the ADL and MxL are normally developed as usually in *Bothriolepis*, but in LDM 43/5082 and 81/30 the AMD overlaps the MxL by a short anterior part of the posterior division of the lateral margin and in LDM 81/262 sutural connection of the AMD plate with the MxL is of *Remigolepis* type. The anterior (dlg1) and posterior (dlg2) oblique dorsal sensory line grooves are well-defined only on the plates of individuals of small and moderate size. In many cases there are variations in the course of the dlg2 noticed, as in *B. canadensis* (Graham-Smith 1978): the dlg2 is short on the right (LDM 81/252) or left (LDM 81/253) side, as well as on both sides, and terminate in front of the postero-lateral margin (LDM 81/28, 81/29, 81/48, 81/250 A, LGI 5/2021). Sometimes the groove swings round, becoming directed anterolaterally and terminates at the AMD/ADL suture (LDM 81/36, 81/372: Figs 67B; 66F). The dlg2 in 20% of the moderate size individuals are not present.

The visceral surface of the AMD shows a slightly lengthened levator fossa (f.retr), which is limited by the low postlevator thickenings (alr). The anterior ventral pit (pt1) and the median ventral ridge (mvr) are low in individuals of small and moderate size, in some specimens the median ventral ridge is very weakly defined. In quite large individuals and especially on the plates, occurring from Ketleri site, on the contrary, the anterior ventral pit is deep and median ventral ridge is rather high. The median ventral groove (grm) is short and usually terminates anteriorly to the posterior margin. The AMD from the Ketleri locality differ a little from specimens, found at Ciecere River, by greater thickness.

The PMD (Figs 68A-C; 69) is narrow with the B/L index about 80-91, 86 on the average. It is almost flat in the anterior part and arched in the posterior part. The width of a narrow anterior margin varies between 37-44% of total breadth of the plate (Lyarskaja incorrectly mentioned

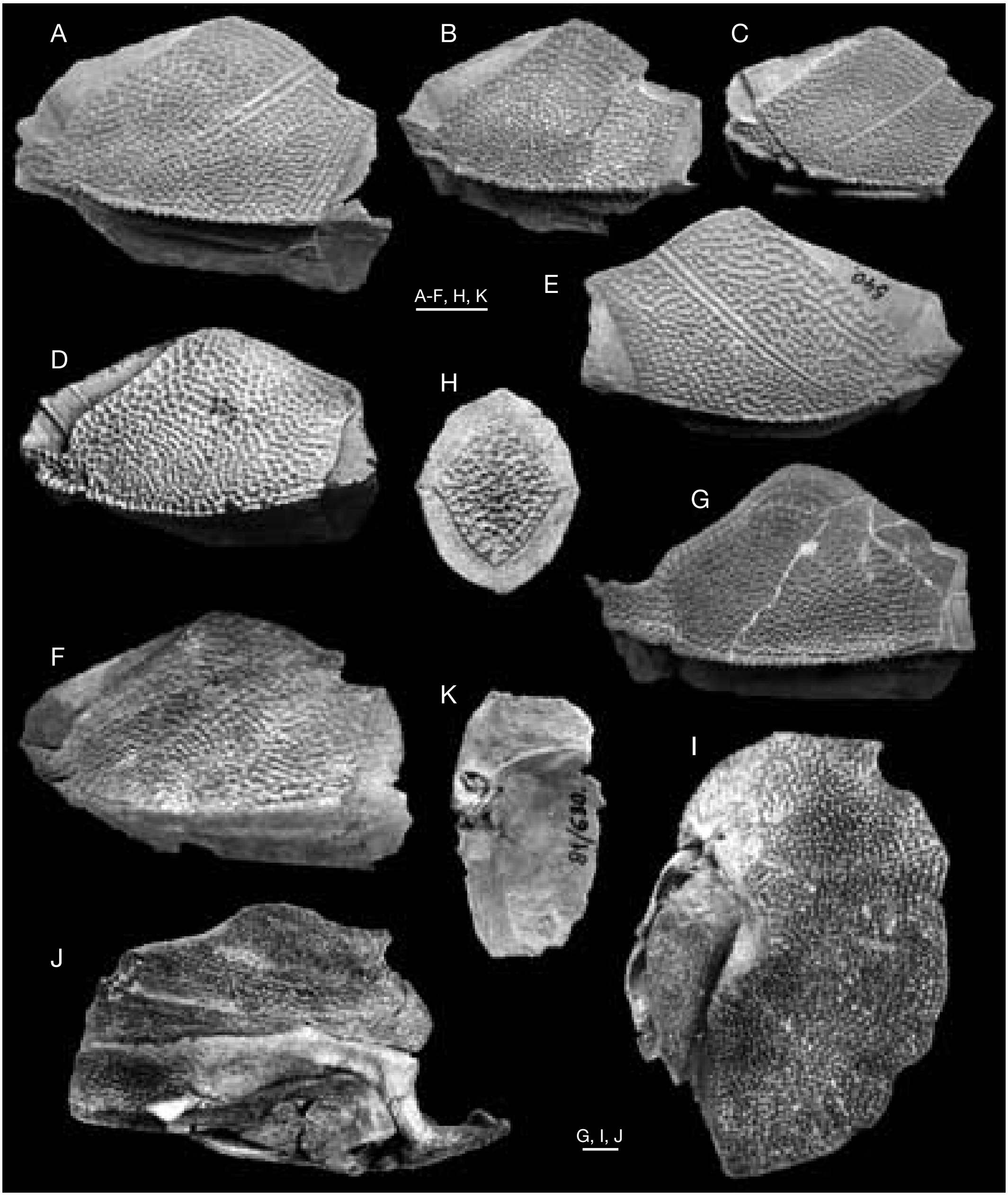

FIG. 71. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**-**G**, MxL; **A**, LDM 81/424; **B**, LDM 81/423; **C**, LDM 81/193; **D**, LDM 81/429; **E**, 81/540; **F**, LDM 81/712; **G**, LDM 81/424; **H**, MV LDM 81/722; **I**, **J**, articulated ADL, AVL, CD1 and CV1 LDM 81/434, in ventral and lateral views; **K**, AVL LDM 81/630 in visceral view. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AVL**, anterior ventro-lateral plate; **CD1**, central dorsal plate 1; **CV1**, ventral central plate 1; **MV**, median ventral plate; **MxL**, mixilateral plate. Scale bars: 10 mm.

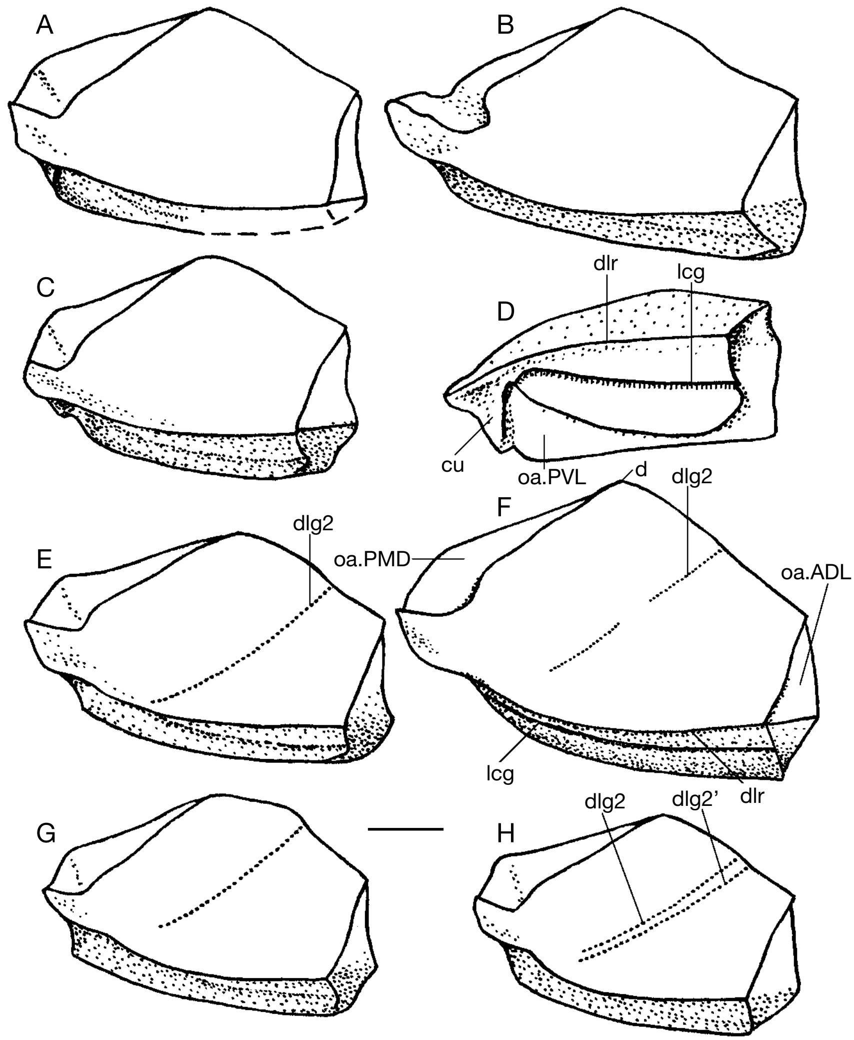

FIG. 72. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, MxL in dorsal (**A**-**C**, **E**-**H**) and lateral (**D**) views; **A**, LDM 81/191; **B**, LDM 81/232; **C**, **D**, LDM 81/196; **E**, LDM 81/190; **F**, LDM 81/7; **G**, LDM 81/210; **H**, LDM 81/211. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro lateral plate; **cu**, postero-ventral ornamented corner; **d**, dorsal corner; **dlg2**, posterior oblique dorsal sensory line groove; **dlg2'**, additional branch of posterior oblique dorsal sensory line groove; **dlr**, dorso-lateral ridge; **lcg**, main lateral line groove; **oa.ADL**, area overlapped by ADL; **oa.PMD**, area overlapped by PMD; **oa.PVL**, area overlapped by PVL. Scale bar: 10 mm.

that the anterior margin is 3-3.5 times shorter than the posterior margin). Specimen LGI 5/2023 (Fig. 69A) shows the abnormally developed overlap area for the MxL, probably arisen as a result of damage of a living animal bone.

The ADL (Figs 68D-H; 70) is slightly shorter than the MxL in articulated armour. The dorsal lamina is relatively narrow and long, and its breadth a little exceeds height of the lateral lamina (Lyarskaja & Savvaitova 1974). The dorsal and lateral laminae of the plate enclosing an angle of 120-125°. Specimen LDM 81/421 shows the dorsal overlap area partly overlaping the AMD.

FIG. 73. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**, articulated AVL and proximal segments of pectoral fin LDM 81/716 in ventral view; **B**, articulated AVL LDM 81/318 and 81/319 in ventral view; **C**, AVL LDM 81/631 in ventral view; **D**, AVL in visceral view with articulated proximal segment of pectoral fin, Nu and Pp in dorsal view, LDM 81/435; **E**, proximal segment of pectoral fin LDM 81/724 in dorsal view; **F**, **G**, proximal segment of pectoral fin LDM 81/723 in ventral and dorsal view; **H**, **I**, CV1 in ventral view; **H**, LDM 81/338; **I**, LDM 81/339; **J**-**K**, ML2 in dorsal view; **J**, LDM 81/634; **K**, LDM 81/334; **L**-**P**, CD1 in dorsal view; **L**, LDM 81/345; **M**, LDM 81/341; **N**, LDM 81/575; **O**, LDM 81/325; **P**, LDM 81/336. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **CD1**, central dorsal plate 1; **CV1**, ventral central plate 1; **ML2**, lateral marginal plate 2; **Nu**, nuchal plate; **Pp**, postpineal plate. Scale bar: 10 mm.

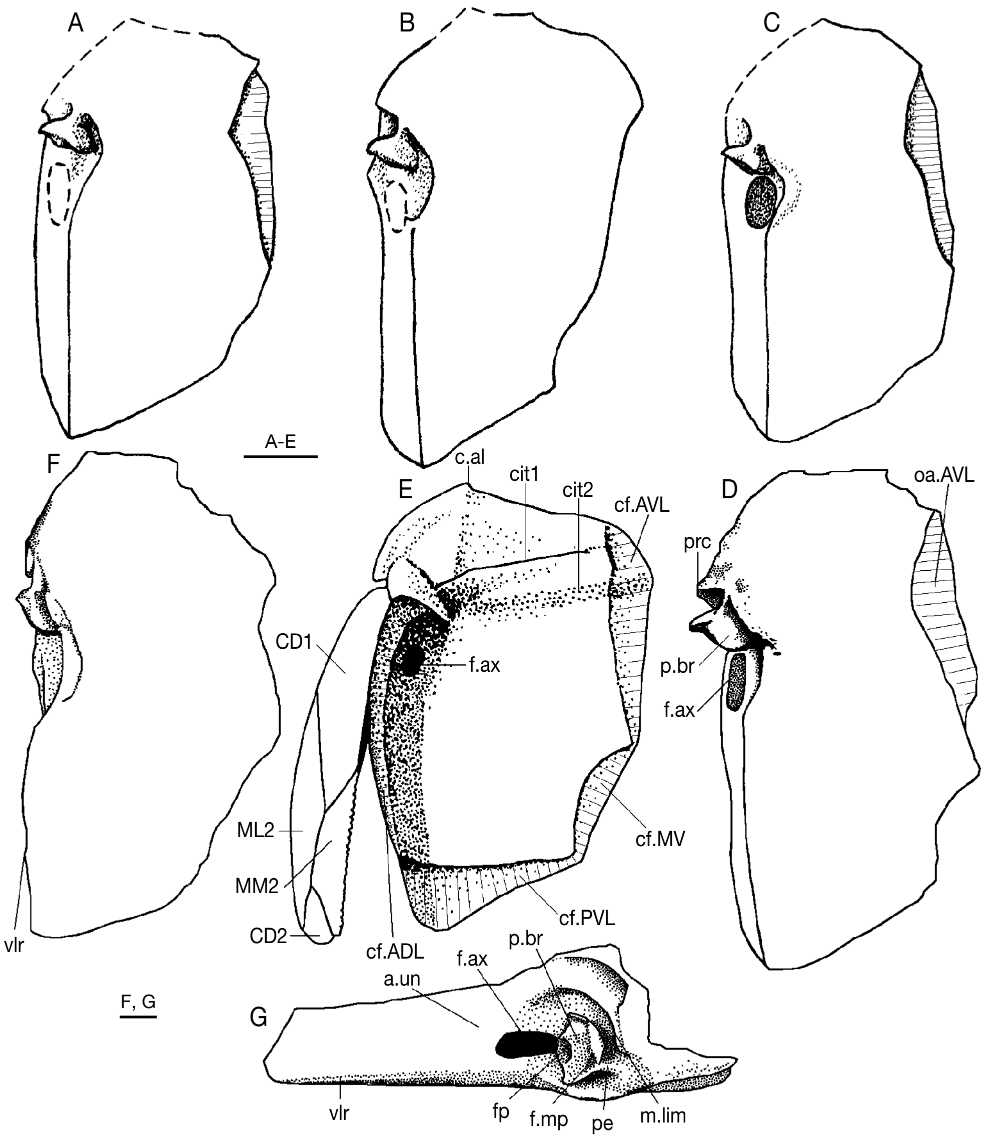

FIG. 74. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974, AVL in ventral (**A**-**D**, **F**), visceral (**E**) and lateral (**G**) views; **A**, LDM 81/3; **B**, LDM 81/4; **C**, LDM 81/70; **D**, LDM 81/631; **E**, AVL with articulated proximal segment of pectoral fin LDM 81/435; **F**, **G**, LDM 81/718. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AVL**, anterior ventro-lateral plate; **MV**, median ventral plate; **PVL**, posterior ventro lateral plate; **a.un**, unornamented area beneath fossa articularis pectoralis; **c.al**, antero-lateral corner of subcephalic division; **CD1**, dorsal central plate 1; **CD2**, dorsal central plate 2; **cf.ADL**, area overlapping ADL; **cf.AVL**, area overlapping AVL; **cf.MV**, area overlapping MV; **cf.PVL**, area overlapping PVL; **cit1**, crista transversalis interna anterior; **cit2**, transverse thickening; **f.ax**, axillary foramen; **f.mp**, protractor area of processus brachialis; **fp**, funnel pit of processus brachialis; **ML2**, lateral marginal plate 2; **m.lim**, margo limitans; **MM2**, mesial marginal plate 2; **oa.AVL**, area overlapped by AVL; **p.br**, processus brachialis; **pe**, pars pedalis of processus brachialis; **prc**, prepectoral corner; **vlr**, ventro-lateral ridge. Scale bars: 10 mm.

The MxL (Figs 71A-G; 72) is moderately long. The dorsal lamina of the plate is less than twice (1.8 on the average) as long as it is broad. Dorsal and lateral laminae enclosing an angle about 111°, but not 135° as claimed Lyarskaja (Lyarskaja & Savvaitova 1974). The lateral lamina

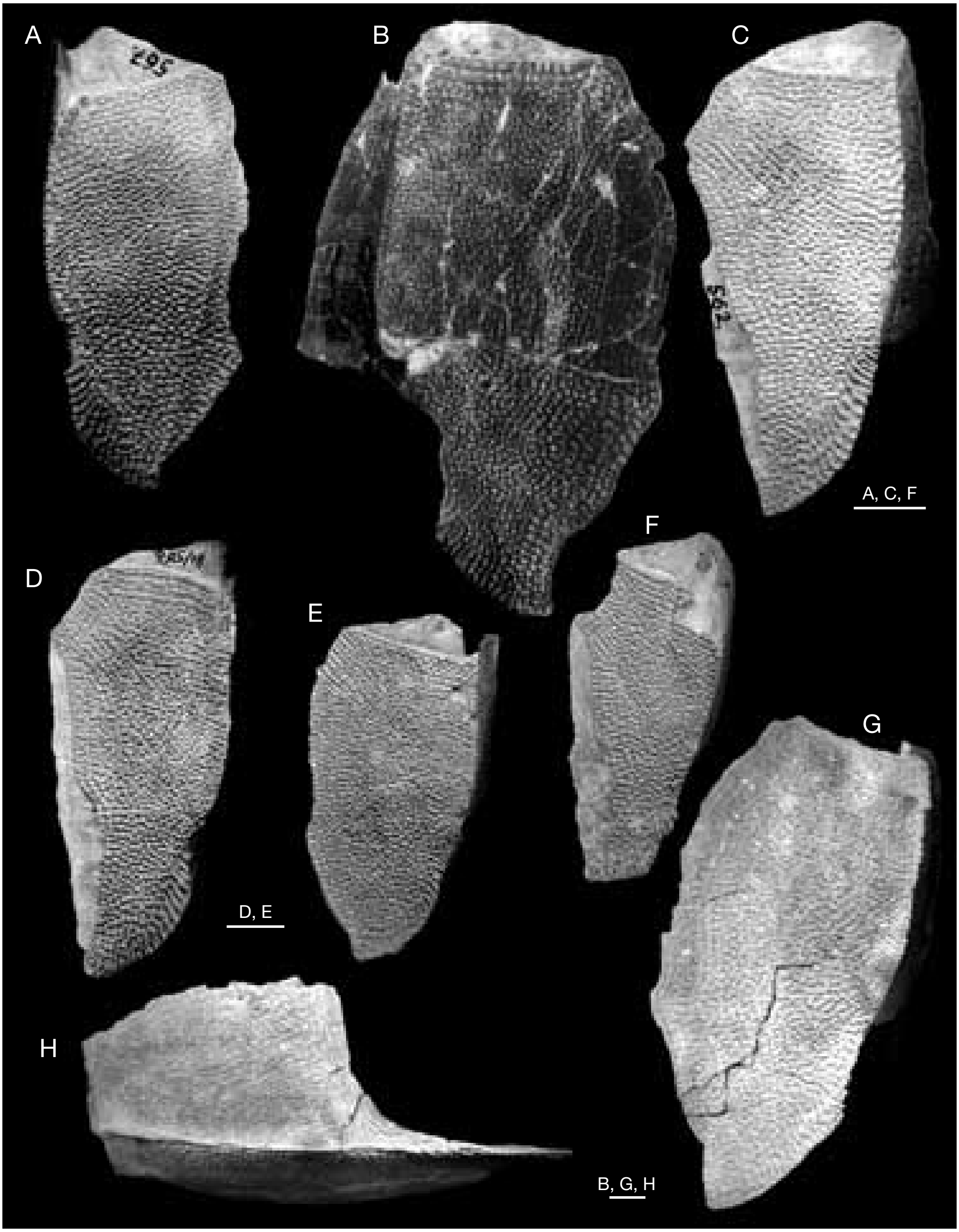

FIG. 75. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**-**F**, PVL in ventral view; **A**, LDM 81/567; **B**, LDM 81/445; **C**, LDM 81/562; **D**, LDM 81/566; **E**, LDM 81/77; **F**, LDM 81/73; **G**, **H**, PVL LDM 81/721 in ventral and lateral views. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviation: **PVL**, posterior ventro-lateral plate. Scale bars: 10 mm.

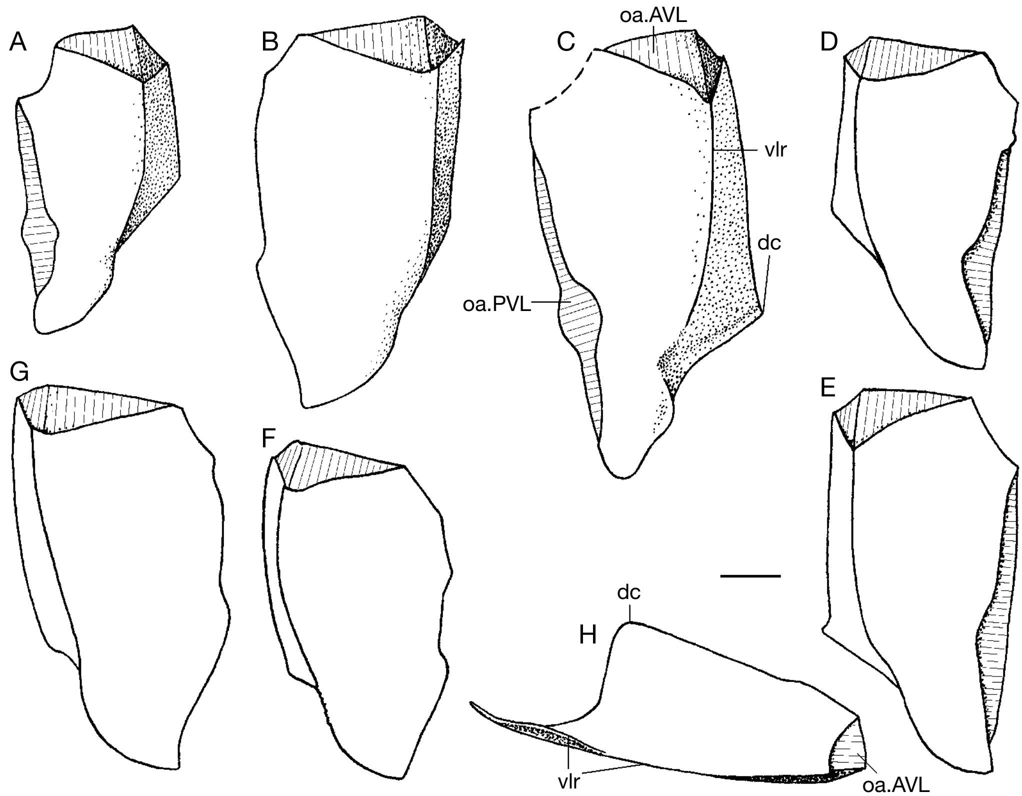

FIG. 76. — *Bothriolepis ciecere* Lyarskaja *in* Lyarskaja & Savvaitova, 1974; **A**-**C**, left-side PVL and D-H, right-side PVL in ventral (**A**-**G**) and lateral (**H**) views; **A**, LDM 81/73; **B**, LDM 81/77; **C**, LDM 81/76; **D**, LDM 81/300; **E**, LDM 81/75; **F**, LDM 81/302; **G**, **H**, LDM 81/78. Ciecere River near Pavāri hamlet, Latvia. Ketleri Formation. Abbreviations: **AVL**, anterior ventro-lateral plate; **PVL**, posterior ventro-lateral plate; **dc**, dorsal corner of lateral lamina; **oa.AVL**, area overlapped by AVL; **oa.PVL**, area overlapped by PVL; **vlr**, ventro-lateral ridge. Scale bar: 10 mm.

is moderately high, 2.9 times as long as it is broad. The posterior oblique sensory line groove (dlg2) is not present almost in a half of specimens. In specimens LDM 81/211 (Fig. 72H) and 81/406, there is an additional branch of the posterior oblique dorsal sensory line groove dlg2', which is parallel to dlg2. The dorso-lateral ridge bears tubercles even in small individuals. The overlap area for the AMD is often restricted to half the length of the antero-dorsal margin (LDM 81/422, 81/423), as in *Remigolepis* (Stensiö, 1931), or to the most part of this margin (LDM 81/424).

The AVL (Figs 73A-D; 74) is of moderate breadth, the ventral lamina is 1.7-2.2 times as long as it is broad. The subcephalic division comprises 17-23% of total length of the ventral lamina. The ventral lamina 2-2.5 times as broad as the lateral lamina high. The lateral lamina is low, 3-3.5 times as long as it is high. Both the right and left AVL could overlap the opposite AVL. The axillary foramen (f.ax) is rather large, slightly elongated and rounded in shape (Lyarskaja & Savvaitova 1974). The visceral surface of the AVL shows the high transverse anterior crista (cit1) running antero-mesially parallel to the low and broad transverse thickening (cit2).

The PVL (Figs 75; 76) has similar proportions to the AVL, as in most *Bothriolepis* species. The ventral lamina is 2-2.6 times as long as it is broad. The subanal division is relatively broad, it occupies about one fifth (18-22%) of the total PVL length. The lateral lamina is high, 1.8-2.4 times long as it is high. The ventral lamina only 1.1 time as broad as the lateral lamina high. The lateral lamina rather steep, the angle between laminae is about 101°, but in no case 130° as indicated by Lyarskaja (Lyarskaja & Savvaitova 1974). Both the right and left PVL could overlap the opposite PVL. The ventro-lateral ridge (vlr) is strongly developed and projects from the plate as a sharp serrated keel along the subanal division. The MV with the L/B index about 1.3 (Fig. 71H).

The pectoral fin (Figs 73E-G; 74E) is represented by many disarticulated bones, and seven specimens showing articulated plates of the proximal segment. There are two examples of the distal segments. Both segments bear prominent lateral and mesial spines. On the proximal segment the spines are large and closely setting. The proximal segment is not as broad as was claimed by Lyarskaja (Lyarskaja & Savvaitova 1974: L/B index about 2), but is 3.5 times as long as it is broad. The CD1 is with L/B index varying from 2.6 to 3.1 (2.9 on the average). The shape and proportions of the other individual plates of the pectoral appendage are shown in Fig. 73.

The ornamentation is reticulate, anastomosing ridges are broken into shorter ridges on the anterior part of the La and Prm and in large specimens also on the Nu and Pp. The ornament on the Sm consists of short ridges and tubercles, on the trunk-armour it is typically reticulate in general. In large specimens, the reticulate ornament retained only on the central part of plates, whereas on the marginal parts of bones the anastomoses between ridges reduse. On the AMD the ornament may consist of ridges parallel to the margins of the plate, but on the MxL and PVL there are short ridges perpendicular to the dorso-lateral or ventro-lateral ridge. The ornamentation of the pectoral appendage is reticulate in general, radially arranged on the CD1. The network ridges bear weak elevations in the points of anastomoses on the ML2 and CV1.

Remarks

Lyarskaja (Lyarskaja & Savvaitova 1974) described two species: *Bothriolepis ciecere* and *B. pavariensis* on a base of material collected in 1971 from the Pavāri locality. She claimed that *B. pavariensis* differs from *B. ciecere* in its 1) larger size; 2) the broader Prm; 3) the shape of Pp; 4) the size and position of the external openings for the endolymphatic ducts; 5) the position and shape of a branches of the posterior oblique sensory line groove; 6) the shape of the AMD (Lyarskaja & Savvaitova 1974). The description of *B. pavariensis* was based on three poorly preserved specimens: part of head-shield LDM 43/337, AMD 43-5082, and ADL 43-5095. In 1978, Lyarskaja collected additional material; the author collections from the type locality, gathered in 1989, 1991, and 1995, and material from the Ketleri locality, collected in 1984, 1995, and 1999, largely expanded *Bothriolepis* materials from the Ketleri Formation. The revision of all material allowed Lukševičs (1991) to suggest that only one species occurs in the Ketleri Formation. Mostly bones are from well-grown individuals of moderate size, but there are also some quite large specimens. All specimen described by Lyarskaja as *B. pavariensis* fit well within the variation row of *B. ciecere*, and there are no gaps in between these two forms neither in the shape and proportions of individual plates, nor in the position of the sensory line grooves. The above mentioned distinctions between *B. pavariensis* and *B. ciecere* could be explained mostly by changes that take place during growth in *Bothriolepis*: size of the plates, shape of the Prm, Pp, AMD; or by considerable intraspecific variation characteristic for *B. ciecere*: the position and shape of the posterior oblique sensory line groove. The following short description is the first full treatment in English, following Lukševičs (1991) and considerably adding details to the description provided by Lyarskaja (Lyarskaja & Savvaitova 1974).

Discussion

Bothriolepis ciecere can be distinguished readily from *B. leptocheira curonica* and *B. jani*

(Lukševičs 1986), other Famennian *Bothriolepis* representatives from the Main Devonian field, and resembles *B. ornata* by some features. *B. ciecere* differs from *B. ornata* in its 1) smaller size; 2) shape and proportions of the Pn and Prm; 3) situation of the lateral pit on the La and postero-lateral corner of otico-occipital depression on the Pn; 4) development of the attachment area for the Sm on the La; 5) broader anterior margin of the AMD; 6) shape of the PMD; 7) strongly developed dorso-lateral and ventro-lateral ridges.

There are no species of *Bothriolepis* from Scotland (Miles 1968) similar to *B. ciecere*. *B. laverocklochensis* Miles, 1968 from the Rosebrae Beds differs from *B. ciecere* in the shape of PMD, absence of the crest on the dorso-lateral ridge and presence of sharply defined dorsal median ridge. *B. wilsoni* Miles, 1968 has well-defined dorso-lateral ridge, however clearly differs from *B. ciecere* in proportions of a head-shield bones, AMD and presence of well-developed dorsal median ridge on AMD, as well as ornament.

The species *B. ciecere* and *B. nielseni* from Greenland are clearly very close morphologically. They are similar in the 1) general proportions of the trunk-armour; 2) development of the dorso-lateral ridge; 3) shape and proportions of individual plates of the trunk-armour; 4) reticulate ornament. Unfortunately, *B. nielseni* is represented only by the holotype which consists of a crushed and flattened trunk-armour and badly preserved parts of the head-shield and pectoral fin (Stensiö 1948). Absence of the description of the head-shield and the poor preservation of the type specimen does not allow to compare both species with sufficient detail. The distinctions between them are insignificant and consist in that in *B. nielseni* 1) the dorsal wall of the trunk-armour is relatively broader; 2) the posterior margin of the AMD is longer; 3) the proximal segment of the pectoral fin is more slender; 4) the ventro-lateral ridge is not bearing the row of tubercles. It seems likely that *B. ciecere* and *B. nielseni* are phylogenetically very close. There is good evidence of a relationship between *B. ciecere* and *B. nielseni*: affinity of their stratigraphical situation, as well as fact, that both *B. ciecere* and *B. nielseni* are the youngest species, the last representatives of *Bothriolepis* in Baltic and Greenland respectively.

Bothriolepis sp. indet. 1
(Figs 77; 78)

MATERIAL EXAMINED. — IEC LP 12-6, a Prm; IEC LP 23-45, anterior part of the AVL; LP 32-1, 23-14, 2 Pn and Nu; IEC LP 23-37, prelateral plate; several fragmentary bones of the trunk armour.

LOCALITY AND HORIZON. — Quarry and mines not far from Zarubino village approximately 25 km SE from Lyubitino town, Novgorod region, Russia; upper Famennian.

DESCRIPTION

IEC LP 12-6 is a relatively large Prm with typical reticulate ornamentation (Fig. 77A, B). It is strongly vaulted both in longitudinal and transverse directions. The plate is broader than it is long, maximum breadth (32.4 mm) exceeds the length (30.4 mm). The gently convex rostral margin with weakly defined rostral angle is about 1.4 time longer than the wavy orbital margin, which bears the clearly defined nasal notches. The infraorbital sensory groove (ifc1) crosses the lateral margin about a fourth of plate length from the rostral margin, but then strongly curves posteriorly and meets the supraorbital canal (soc) behind the middle of the plate. The preorbital recess is of trifid type.

The Nu IEC LP 23-14 (Figs 77C; 78A) is moderately broad as it is preserved, bears the moderately broad obtected nuchal area and well-defined right lateral margin. The plate is broadest across the lateral corners. The posterior margin is almost straight and possess no posterior process. The central sensory line groove is clearly distinct.

The Pn (Figs 77D; 78B-D) is of moderate breadth, L/B index 80-96. The lateral division of the Pn is relatively narrow composing 48% of the general breadth of a plate. The postero-

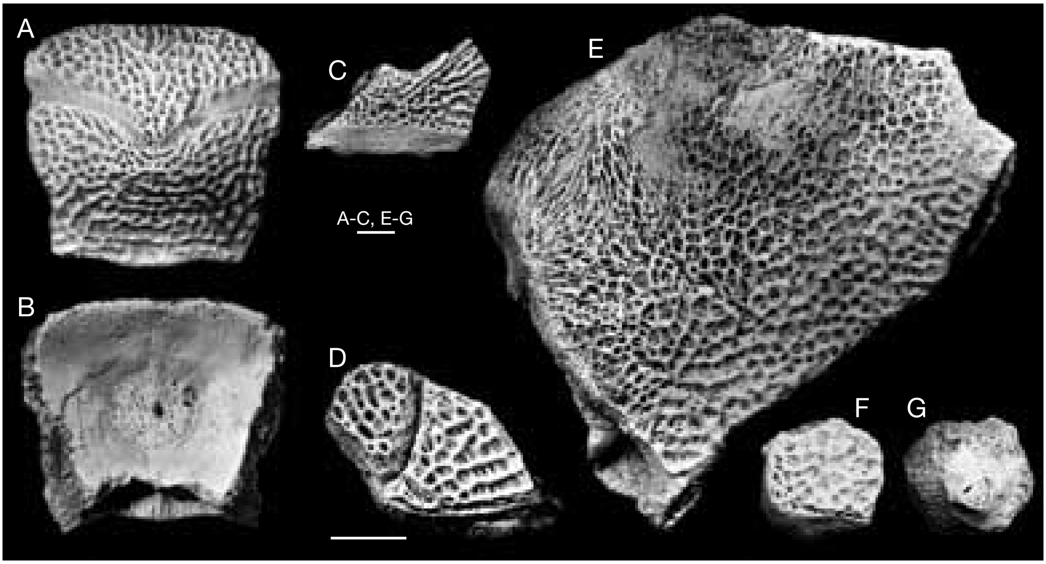

FIG. 77. — *Bothriolepis* sp. indet. 1; **A**, **B**, Prm IEC LP 12-6 in dorsal and visceral view; **C**, fragmentary Nu IEC LP 23-14; **D**, Pn IEC LP 23-1; **E**, anterior part of the AVL IEC LP 23-45 in ventral view; **F**, **G**, prelateral plate IEC LP 23-37 in dorsal and visceral view. Quarry near Zarubino village, Novgorod region, Russia. Upper Famennian. Abbreviations: **AVL**, anterior ventro-lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate; **Prm**, premedian plate. Scale bars: 5 mm.

lateral corner of otico-occipital depression (pr.po) is rounded and extends laterally over the middle of the Pn's posterior margin.

The AVL IEC LP 23-45 (Fig. 77E) is of moderate breadth as it is preserved. The subcephalic division seems to be relatively short. The anterior lateral corner of subcephalic division is situated laterally from the middle between the median and lateral margins; it is developed into a short process. Fragmentary MxL and PVL show a well-developed keel on the dorso-lateral and ventro-lateral ridges.

The ornamentation is reticular, consisting of large pits and quite coarse anastomosing ridges.

REMARKS

All specimens from Zarubino locality, collected by amateur collector, were grouped together because of typical reticular ornamentation with large pits between ridges.

Bothriolepis sp. indet. 1 resembles *Bothriolepis ciecere* in several features: 1) shape and proportions of the Prm; 2) proportions of the Pn; 3) the position of the postero-lateral corner of otico-occipital depression; 4) similarly strongly defined dorso-lateral and ventro-lateral ridges on the trunk armour; 5) similar ornamentation, but differs in other shape of the Nu and Pn, as well as in more strongly arched Prm.

Genus *Grossilepis* Stensiö, 1948

TYPE SPECIES. — *Grossilepis tuberculata* (Gross, 1941).

DIAGNOSIS. — Bothriolepididae in which the AMD of an almost uniform breadth behind the postlevator processes, and normally overlaps both the ADL and MxL. The ADL and MxL also fairly uniform in width throughout their extent.

Grossilepis tuberculata (Gross, 1941)
(Figs 79; 80)

Bothriolepis tuberculata Gross 1941: 32-57, abb. 25, 26A-G, 27A-C, 28-43; taf. 18-28.

Bothriolepis cellulosa (Pander) – Gross 1932: 24 (*p.p.*); 1933: 36-39, taf. 4, fig. 5 (*p.p.*). — Obruchev 1947: pl. LV, fig. 4.

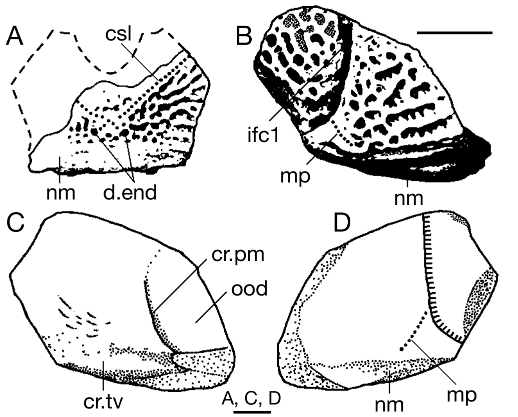

FIG. 78. — *Bothriolepis* sp. indet. 1; **A**, reconstruction of the Nu IEC LP 23-14; **B**, Pn IEC LP 23-1; **C**, **D**, Pn IEC LP 23-46 in visceral and dorsal view. Quarry near Zarubino village, Novgorod region, Russia. Upper Famennian. Abbreviations: **Nu**, nuchal plate; **Pn**, paranuchal plate; **cr.pm**, paramarginal crista; **cr.tv**, transverse nuchal crista; **csl**, central sensory line groove; **d.end**, opening of canal for endolymphatic duct; **ifc1**, principal section of infraorbital sensory line; **mp**, middle pit-line groove; **nm**, obtected nuchal area; **ood**, otico-occipital depression. Scale bars: 5 mm.

Grossilepis tuberculata (Gross) – Stensiö 1948: 524-534, text-figs 26L, 28E, 35F, 36C-E, 39D, 41D, 43E, 44F, 45H, 47D, 48D, 53D, 266-271.

HOLOTYPE. — AMD kept in SMNH (Gross 1941: abb. 30F, taf. 21, fig. 1).

MATERIAL EXAMINED. — LDM 65/77, MxL; NHM 17827, La; NHM 17811, 17817, 17820, three PMD; NHM 17812, PVL; LUGM, several unnumbered specimens including AMD, PMD, La plates is aaditional to that described by Gross (1941) and Stensiö (1948).

LOCALITIES AND HORIZON. — The type locality is an outcrop of dolomite, dolomite marl and clay at the bank of Pērse River near Koknese, Latvia; The lower Frasnian Pļaviņas Formation. This species was found in the Snetnaya Gora Member in several localities in western and eastern Latvia: outcrops along Daugava River from Kaktiņi to the ruins of Koknese castle, exposures at Amata River not far from Kārļi and along Mazā Jugla and Lielā Jugla Rivers, outcrops at Venta River near Kuldīga and at Riežupe River (Sorokin 1978), Lithuania: borehole Berčiunai, 73-76 m deep, borehole Pakapiai, 78.2-80.3 m deep, and Pskov region of Russia: outcrop at the right bank of Velikaya River near Piskovichi hamlet, Snetnaya Gora, Pskov and Chudovo Beds of Russia. The remains of *G. tuberculata* are very rare in the middle part of the Pļaviņas Formation (Atzele and Sēlija Members, which corresponds to the Pskov Beds in Russia) and until now reported only from eastern Latvia (Sorokin 1978).

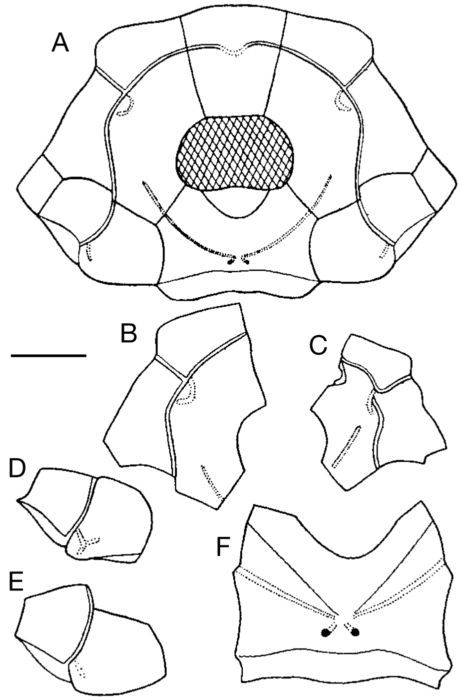

FIG. 79. — *Grossilepis tuberculata* (Gross, 1941); **A**, reconstruction of the head-shield; **B**, **C**, La; **D**, **E**, Pn; **F**, Nu (from Gross 1941: abb. 29 II, 27A, 27C, 26B, 26A, 25A respectively). Pērse River near Koknese (Kokenhusen), Latvia. Pļaviņas Formation. Abbreviations: **La**, lateral plate; **Nu**, nuchal plate; **Pn**, paranuchal plate. Scale bar: 10 mm.

DIAGNOSIS. — Relatively small bothriolepidoid with estimated length of dorsal wall of trunk armour reaching about 9 cm. Head-shield moderately vaulted with anterior margin much shorter than total breadth of the plate. Postero-lateral corners of head-shield extends anteriorly to the level of the orbital fenestra posterior margin. Nu of moderate width, L/B index of about 61-73, usually with concave posterior margin bearing the median process, shallow postpineal notch on the anterior margin, slightly pronounced lateral and postero-lateral corners. Pn with broad lateral division. Tergal angle situated between the anterior and middle thirds of the AMD length. Posterior margin of AMD very broad. Dorsal median ridge normally developed from the tergal angle backwards to the posterior corner of PMD. Dorsal corner slightly pronounced or sometimes even not be clearly identifiable. Pectoral fin fairly slender, proximal segment from 4.5 to slightly more than 5 times as long as broad. Lateral spines of the pectoral fin numerous, small, closely set and obtuse. Ornament consists of numerous closely and irregularly set pointed tubercles in well-grown individuals.

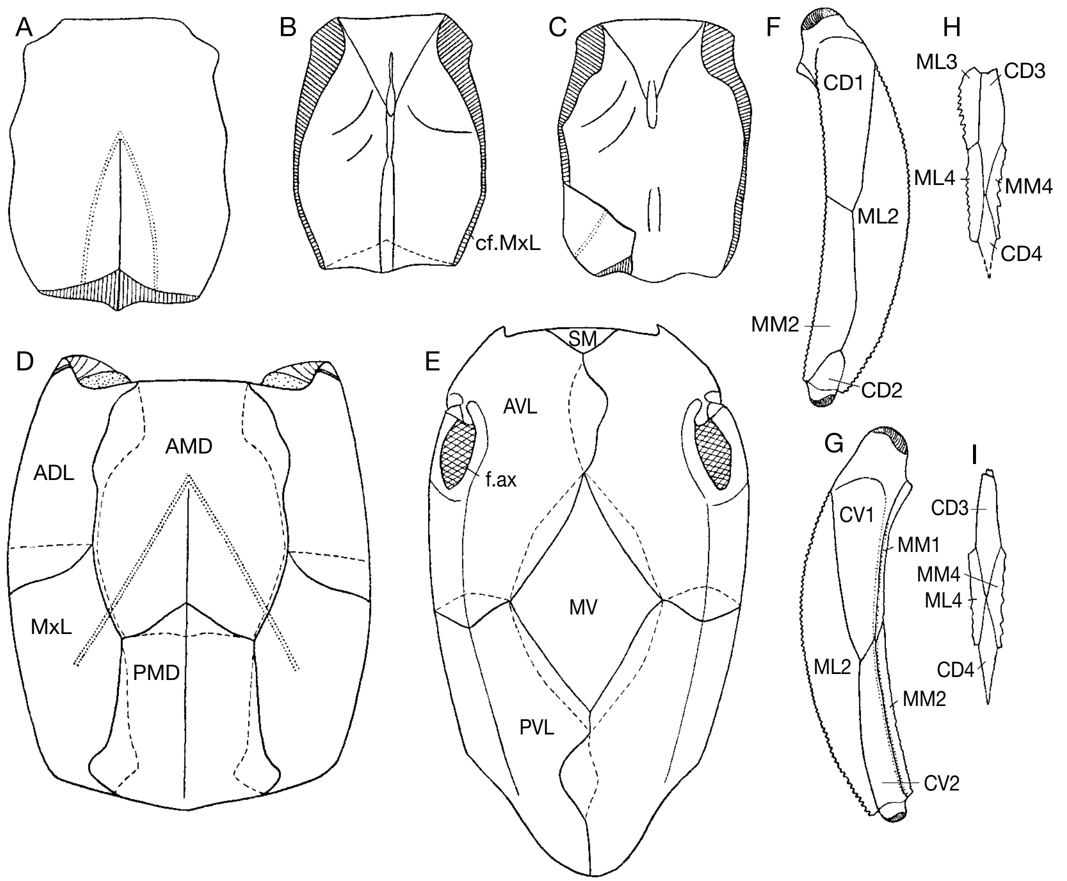

FIG. 80. — *Grossilepis tuberculata* (Gross, 1941); **A**, **B**, AMD in dorsal (**A**) and visceral (**B**) views; **C**, specimen showing visceral and partly remained dorsal side of the AMD; **D**, reconstruction of dorsal wall of the trunk armour; **E**, reconstruction of ventral wall of the trunk armour; **F**, **G**, reconstruction of proximal segment of pectoral fin in dorsal and ventral views; **H**, **I**, parts of distal segment of pectoral fin in dorsal view. From Gross 1941: abb. 30F, 30A, 30D, 36, 37, 43A, 43B, 43F, 43H respectively. Pērse River near Koknese (Kokenhusen), Latvia. Pļaviņas Formation. Abbreviations: **ADL**, anterior dorso-lateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD1**-**4**, dorsal central plates 1 to 4; **CV1**, **2**, ventral central plates 1 and 2; **ML2**-**4**, lateral marginal plates 2 to 4; **MM1**, **2**, **4**, mesial marginal plates 1, 2 and 4; **MV**, median ventral plate; **MxL**, mixilateral plate; **PMD**, posterior median dorsal plate; **PVL**, posterior ventro-lateral plate; **SM**, semilunar plate; **cf.MxL**, area overlapping MxL; **f.ax**, axillary foramen.

REMARKS

This species is well-described by Gross (1941) and Stensiö (1948). Their descriptions are based on a large collection of the placoderm and other fish remains kept at Swedish Museum of Natural History, Stockholm. Although little new material is available that has not been described before, the descriptions of Gross and Stensiö can be added, providing a new definition of this species, as the definition of *Grossilepis tuberculata* suggested by Stensiö (1948: 523-524) was the same as that of the genus *Grossilepis*.

DISCUSSION

The comparison of *Grossilepis tuberculata* with *G. spinosa* is provided below the description of the latter. *G. tuberculata* differs well from *G. brandi* Miles, 1968 in its relatively narrower Nu and a proportions of the anterior and posterior divisions of the lateral margin of this plate.

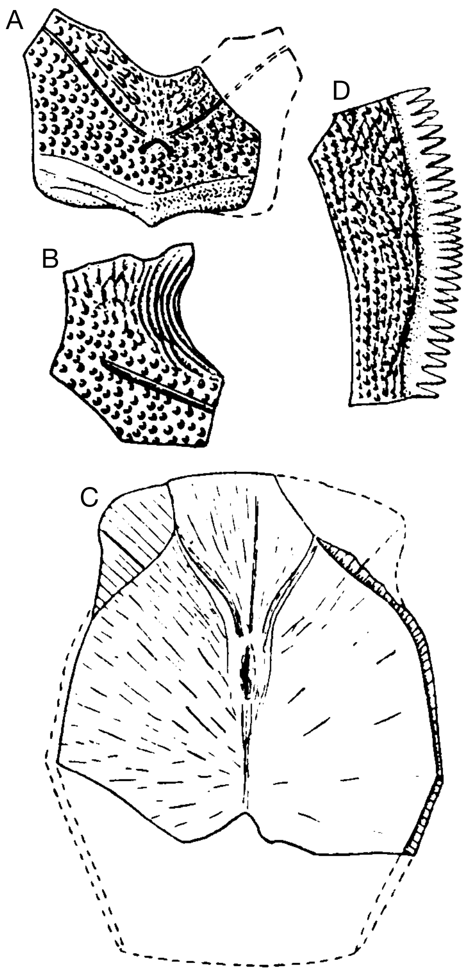

FIG. 81. — *Grossilepis spinosa* (Gross, 1942); **A**, Nu; **B**, fragmentary La; **C**, anterior part of AMD in ventral view; **D**, ML2. From Gross 1942: abb. 9A-D. Imula River near Lankserde hamlet, Latvia. Ogre Formation. Abbreviations: **AMD**, anterior median dorsal plate; **ML2**, lateral marginal plate 2; **La**, lateral plate; **Nu**, nuchal plate.

Grossilepis spinosa (Gross, 1942) (Fig. 81)

Bothriolepis spinosa Gross 1942: 418-420, abb. 9A-D.

Grossilepis(?) *spinosa* (Gross) – Stensiö 1948: 615.

HOLOTYPE. — Nu kept in SMNH.

MATERIAL EXAMINED. — The specimens described and illustrated by Gross (1942), kept at SMNH.

LOCALITIES AND HORIZON. — The type locality is an outcrop containing red-grey sandstone at the right bank of Imula River near Ģenduļi and Bienes hamlets, Latvia. Some specimens were collected from the Velna Ala site at the left bank of Abava River. The middle Frasnian Ogre Formation.

DIAGNOSIS. — A small bothriolepidoid with estimated length of dorsal wall of trunk armour reaching about 6 cm. Nu is moderately wide with B/L index of 62 in holotype, with convex posterior margin bearing the sharp median process, shallow postpineal notch on the anterior margin, slightly pronounced posterolateral corners and well-defined lateral corners. Clearly defined lateral corner is slightly pronounced. Lateral spines of ML2 are strikingly long and pointed. Ornament consists of numerous closely and irregularly set tubercles.

DISCUSSION

Grossilepis spinosa resembles *Grossilepis tuberculata* by several features, but could be readily distinguished from it in its 1) other shape of the Nu and its posterior margin; 2) character and shape of strongly developed long lateral spines of the proximal segment of pectoral fin. *Grossilepis spinosa* differs well from *G. brandi* in its relatively narrower Nu and a proportions of the anterior and posterior divisions of the lateral margin of this plate.

REMARKS

This species was established by Gross (1942) as belonging to the genus *Bothriolepis*, but Stensiö (1948) suggested it is fairly close to *Grossilepis tuberculata. Grossilepis spinosa* shows some features characteristic for the genus *Grossilepis* as the shape of the AMD, sutural connections between the AMD and MxL, as well as tuberculate ornamentation.

INTERRELATIONSHIPS OF BALTIC BOTHRIOLEPIDS

There is no widely adopted classification of placoderms (Obruchev 1964; Miles 1968; Denison 1978, 1983; Young 1984a; Goujet & Young 1995; Janvier 1996); placoderm groups are being subdivided using strongly differing criteria. The classification of Obruchev (1964) has been used in the Russian paleoichthyological literature (e.g., Karatajūte-Talimaa 1963, 1966; Malinovskaya 1977; Lyarskaja 1981) with the class Placodermi divided into two subclasses: Arthodira and Antiarcha including respectively ten and two orders (Asterolepidida and Remigolepidida). Antiarchs have been regarded as order (Denison 1978, 1983), or sister group of Euarthrodira (Young 1984), sister group Palaeacanthaspida (Goujet 1984) or Arthrodira and some other groups of Placodermi, but not all Arthrodira *sensu* Obruchev (Gardiner 1984). Recently Goujet & Young (1995) proposed a new scheme of the interrelationships of placoderms. According to their analysis, the Antiarcha are placed between the tesserate forms (Acanthothoraci and Rhenanida) and other, more advanced placoderms.

Novitskaya (1986) claimed that she found the outer hypophyseal opening in two specimens of *Asterolepis ornata*. This opening, she claimed, pierces "the bottom of praenasal pit" under the nasal openings and is situated between them (Novitskaya 1986: fig.1zh; Novitskaya & Karatajūte-Talimaa 1989: fig. 3; pl. 1, fig. 1). Reexamination of the described specimens and additional excellently preserved material on *Asterolepis ornata* kept in the LDM reveals no evidence of such a canal. The slight pit between the Prm and Ro in described specimen is probably a misinterpreted preparation mark in the remained clay matrix. The praenasal (anterior) wall of the rostral plate is closely fitted to the vertically directed posterior wall of the Prm, leaving no place for a canal (Lukševičs 1999b).

Miles (1968) divided the antiarchs into suborders Asterolepidoidei, Bothriolepidoidei and Yunnanolepidoidei. Denison (1978) considered yunnanolepids as belonging to the family Bothriolepididae, and additionally accepted two more families: Asterolepididae and Sinolepididae. Janvier & Pan Jiang (1982), following Miles, regarded *Yunnanolepis* Liu, 1963 as a very primitive and separate genus, characterized by absence of *processus brachialis*, and referred it to a separate order. The other antiarchs were united into group Euantiarcha including Sinolepidida, Bothriolepidida and Asterolepidida.

Young (1984a) also supported such a scheme, suggesting four groups in the antiarch cladogram: yunnanolepids, sinolepids, asterolepidoids and bothriolepidoids, uniting the three latter into an euantiarch group.

Zhang Guorui (1984) introduced the new antiarch order Procondylolepiformes, including the new family Procondylolepidae. Later, Pan *et al.* (1987) referred the family Procondylolepidae to Euantiarcha. Tong-Dzuy & Janvier (1990) noted that *Procondylolepis* from China is closely related or similar to *Chuchinolepis* Chang, 1978 from Vietnam; both are characterized by a weakly developed primitive *processus brachialis*. They therefore referred *Procondylolepis* Zhang, 1984 to the family Chuchinolepidae.

Zhang Guorui & Young (1992) analysed the distribution of several characters within 13 genera, producing four cladograms of possible bothriolepidoid interrelationships.

Adding recently described taxa to the scheme proposed by Young (1984a), their phylogenetic position is tentatively envisaged in Fig. 82. Four genera are concerned, each author referring them to bothriolepid: *Vietnamaspis* described by Long *et al.* (1990), *Jiangxilepis* from China (Zhang & Liu 1991), *Tenizolepis* from Kazakhstan (Malinovskaya 1977), *Kirgisolepis* from Kirgizia (Panteleyev 1993) are also included here. Nevertheless, *Tenizolepis* and *Kirgizolepis* are characterized by primitive features distinguishing them from *Bothriolepis* but being closer to *Dianolepis* Chang, 1965: Pp is broad and makes contact with the La; the relatively short pectoral appendages do not reach the posterior margin of the trunk-shield; and CD1 has a common suture with CD2.

Several recent publications have been dealt with the interrelationships of placoderms and particularly bothriolepids (Long 1983; Long & Werdelin 1986; Young 1984a, 1988). Young (1988) paid great attention to three aspects of bothriolepid antiarch morphology: the structure of preorbital recess, submarginal attachment to

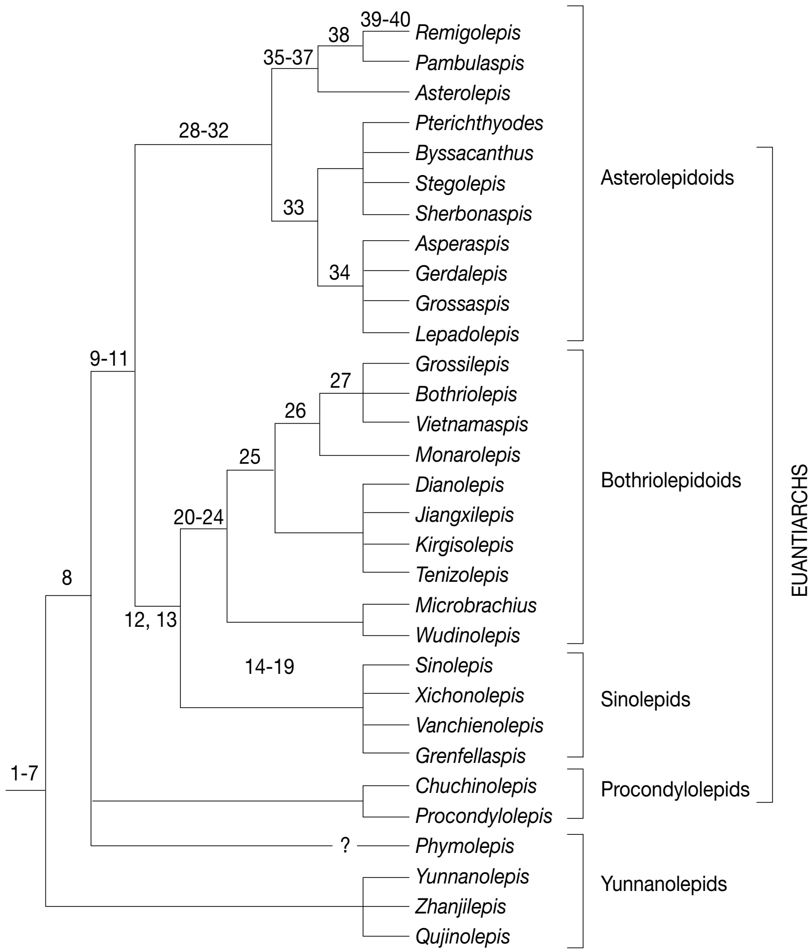

FIG. 82. — Cladogram for antiarch genera, modified after Young (1988). For synapomorphies 1-40 see Young (1984).

the skull, and ontogenetic change in the shape of the AMD. He suggested four types of preorbital recess and named them as "simple", "trilobate", "pentagonal", and "trifid". The simple recess is the semicircular form of Long (1983). Stensiö (1948) and Miles (1968) have described the preorbital recess of the most simple shape without lateral and median extensions or "horns" as the "*canadensis*-type" because it was first described in detail for *B. canadensis*. Among the Baltic species the simple recess is found in earliest representatives of the genus*: B. prima, B. obrutschewi, B. cellulosa, B. traudscholdi,* and from the other areas it is known in the Antarctic species *B. askinae* Young, 1988, as well as in *B. volongensis* Lyarskaja & Lukševičs, 1999 (see Lukševičs & Sorokin 1999) from North Timan. The trilobate recess, which is distinguished from the simple recess by having an anteriorly protruded middle part on the Prm, is so far unknown in Baltic species, being reported from *B. hydrophyla* and *B. alvesiensis* Stensiö, 1948 from Scotland, and *B. barretti* Young, 1988 from the Antarctic. The pentagonal recess has well-defined lateral and median angles, the lateral angle being about 90°. This type of recess is

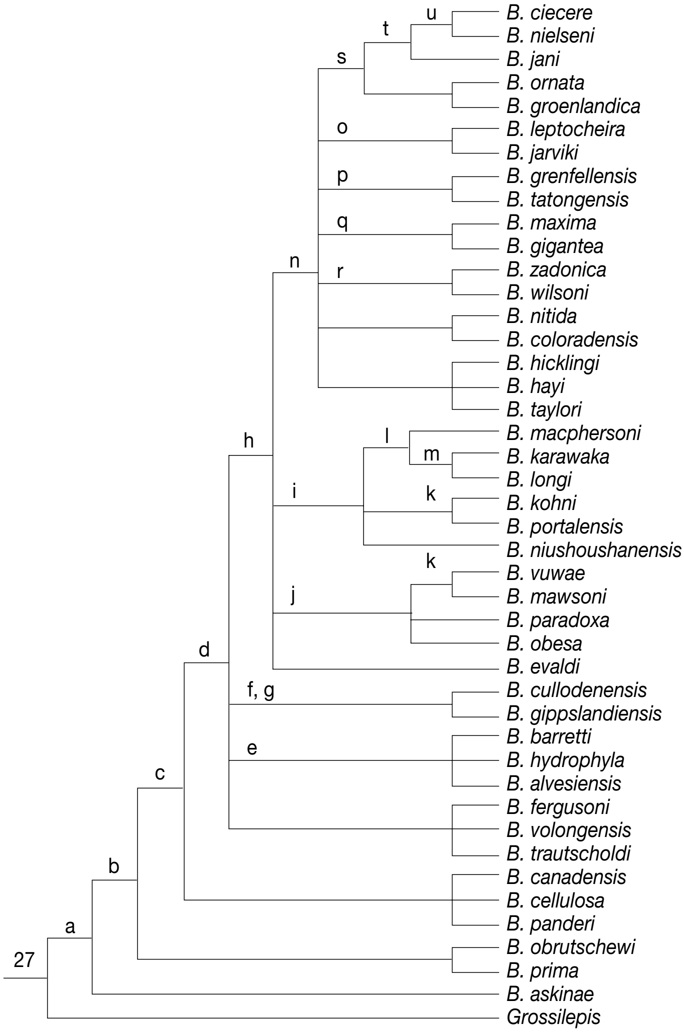

FIG. 83. — Cladogram for various species of *Bothriolepis*, added by bothriolepids from Baltic area and Australia (Johanson 1997, 1998; Johanson & Young 1999), and modified after Young (1988). Synapomorphies are: **a**, AMD in adults broadest across lateral corners, and MxL broadest through its dorsal corner; **b**, lateral corners on AMD appear early in ontogeny; **c**, point contact between MM1 and CV2 of pectoral fin, to separate CV1 from MM2; **d**, axillary foramen longer than high; **e**, trilobate preorbital recess; **f**, trunk armour with pronounced median dorsal crest; **g**, short, deep Sm; **h**, pentagonal preorbital recess; **i**, anterior Sm attachment supported by a separate ridge in transverse lateral groove; **j**, squarish Nu with convex anterior division of the lateral margin and short postero-lateral corners; **k**, elongation of preorbital region of skull; **l**, separate triangular and ventrally-facing attachment surface for Prl on La; **m**, anterior portion of posterior submarginal attachment covers spiracular groove; **n**, trifid preorbital recess; **o**, slender proximal segment of pectoral fin; **p**, orbital margin of Pp at the level of lateral corners of head-shield; **q**, branch of the infraorbital sensory line diverging on the Prl parallel to rostral margin of head-shield; **r**, massive, low and broad median dorsal crest on AMD; **s**, thickened bone edges on orbital margins of Prm and La plates; **t**, crista transversalis anterior transversely oriented parallelly to cit2 on visceral surface of ventral lamina of AVL; **u**, ventro-lateral ridge is making a keel. Abbreviations: **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CV1**, **2**, ventral central plates 1 and 2; **MM2**, mesial marginal plate 2; **MxL**, mixilateral plate; **cit2**, transverse thickening; **La**, lateral plate; **Nu**, nuchal plate; **Pp**, postpineal plate; **Sm**, submarginal plate.

known in many Antarctic species such as *B. portalensis* Young, 1988, *B. karawaka* and *B. macphersoni* (see Young 1988). The trifid recess was previously described as the "*groenlandica*-type" (Stensiö 1948; Miles 1968). It differs from the pentagonal recess in the more acute and elongated lateral angles, and the development of angular indentations on the anterolateral margins of the recess, forming three projections into the Prm and La. The trifid recess is known in several species of *Bothriolepis* from Baltic, such as *B. maxima, B. leptocheira, B. ornata,* and *B. ciecere*. *B. jani* has probably the recess of intermediate type between pentagonal and trifid types, with short lateral horns, but broad anterior projection. The trifid recess have been reported also in *B. jarviki, B. gigantea, B. leptocheira, B. hayi,* and *B. hicklingi* from Scotland (Miles 1968), *B. nitida* (Leidy, 1856) from Pennsylvania (Young 1988), *B. groenlandica* from East Greenland (Stensiö 1948), *B. grenfellensis* Johanson, 1997, *B. yeungae* Johanson, 1998 and probably *B. tatongensis* Long & Werdelin, 1986 from Australia.

The simple recess is considered to be plesiomorphic (Long 1983; Young 1988). Regarding the occurrence of this type of recess among the Baltic species, it is known only from specimens belonging to the possibly uppermost Middle Devonian or lowermost Upper Devonian Amata Formation (*B. prima, B. obrutschewi*), and lower/middle Frasnian (*B. cellulosa*, *B. traudscholdi*). The trifid recess appears in Baltic species of *Bothriolepis* rather later than in Australian forms: recess of trifid type occurs for the first time in *B. maxima* from the upper Frasnian, whereas among the bothriolepids from western Australia "*Bothriolepis* sp. from Gogo [...] (Young 1984b), represents one of the earliest well-dated occurrences (early Frasnian) of the trifid recess" (Young 1988: 111).

Long (1983) published a cladogram based mainly on the preorbital recess shape, including 18 species of *Bothriolepis*. Young (1988) added the Antarctic species to this cladogram and, using several additional characters, analyzed the interrelationships of 37 species in total.

A list of 20 characters (see Appendix) summarizing their distribution in *Bothriolepis* species from Baltic and NW Russia has been established in order to run a phylogenetic analysis. Unfortunately the unique and pectinate tree resulting from the PHYLIP analysis has not been retrieved with parsimony softs (PAUP, etc.). So in agreement with the editor we decided not to publish this result until a more complete and testable parsimony analysis has been run.

A new version of the interrelationship cladogram for the best known bothriolepids has been completed by including in Young's cladogram the Baltic species of *Bothriolepis*. Unfortunately several bothriolepid taxa from China and Kazakhstan have been poorly described and could therefore not be included in the analysis. Interrelationships among 44 bothriolepidid taxa (*Grossilepis tuberculata* and 43 species of *Bothriolepis*) are presented in Fig. 83 (the last appearance of the cladogram has been prepared manually due to insufficient amount of analysed characters and too large number of species). *Grossilepis tuberculata* has been used in the analysis as a sister group of *Bothriolepis*. It differs from the species of *Bothriolepis* in the absence of lateral corners of the AMD. Among the other taxa in the analysis, *B. askinae* shows unusual changes of shape of the trunk armour plates during ontogeny with the AMD developing the lateral corners at a late stage (Young 1988). All the other *Bothriolepis* probably have lateral corners of AMD which appear earlier in ontogeny and Young (1988) has suggested this feature is a synapomorphy of these species which compose a monophyletic group.

Bothriolepis prima and *B. obrutschewi* have pectoral fins with the CV1 making contact with the MM2. All the remaining species possess a point contact between the MM1 and CV2 of the pectoral fin, to separate the CV1 from the MM2.

Most species of *Bothriolepis* have an axillary foramen longer than high. Species of *Bothriolepis* with a simple recess and elongated axillary foramen could be subdivided into two groups. *B. cullodenensis* Long, 1983 and *B. gippslandiensis* Hills, 1929 could be united into a separate clade sharing a pronounced median dorsal crest on the trunk armour (Long & Werdelin 1986; Young 1988). Within this group, *B. gippslandiensis* acquires through reversal a character otherwise seen in more primitive members of the genus like *B. prima* and *B. obrutschewi*, namely a CV1-MM2 contact in the pectoral fin.

About three quarters of all the species of *Bothriolepis* included in the analysis have the more complex preorbital recess. As it is already mentioned, *B. barretti*, *B. hydrophyla* and *B. alvesiensis* have a trilobate preorbital recess. The members of this clade have been reported from Scotland and Antarctic. The group possessing the pentagonal preorbital recess is subdivided into four clades. *B. evaldi* seems to be the most primitive member of the group. The largest clade is characterized by the presence of a trifid preorbital recess. The second largest clade is characterized by the nature of the cheek attachment, which was proposed by Young (1988) as useful for delineating species groups within *Bothriolepis*. *B. macphersoni*, *B. karawaka*, *B. kohni*, *B. portalensis* Young, 1988 from Antarctica, and *B. niushoushanensis* Pan *et al.*, 1980 from North China, have an anterior Sm attachment supported by a separate ridge in the transverse lateral groove on the visceral surface of the head shield. Among them, *B. macphersoni* and *B. karawaka* possess a separate triangular and ventrally-facing attachment surface for the Prl on the lateral margin of the La. The next clade of *Bothriolepis* having a pentagonal preorbital recess is characterized by the squarish Nu with convex anterior division of the lateral margin and short postero-lateral corners, a set of features first used by Young (1988) in his analysis. This clade includes two species from Scotland, namely *B. obesa* Traquair, 1888 and *B. paradoxa*, as well as two taxa from Antarctica (*B. mawsoni* Young, 1988 and *B. vuwae* Young, 1988). Somewhat surprisingly, the analysis fails to unite *B. kohni* and *B. portalensis* with *B. vuwae* and *B. mawsoni*, even though all share an elongated preorbital region of the skull with a long and narrow Prm.

Finally it should be noted that the group of *Bothriolepis* species with a trifid preorbital recess contains members from both Laurussia and Gondwana, and could be delineated using such a characters as the elongation of the pectoral fin, position of the branch of the infraorbital sensory line diverging on the Prl, the presence of a massive, low and broad dorsal crest on the trunk armour, and the appearance of thickened bone edges on the orbital margin of the Prm and La. The last feature probably appears twice during the phylogenetic development of the group, as it occurs not only in those species of *Bothriolepis* which have a trifid preorbital recess and appear very late, in the middle-late Famennian (*B. ornata*, *B. groenlandica*, *B. jani*, *B. nielseni*, *B. ciecere*), but also in *B. macphersoni, B. karawaka* and *B. niushoushanensis*.

The proposed result of the analysis fits well with those presented by Young (1988). The phylogenetic analysis of *Bothriolepis* species from several continents leads to the conclusion that an isolation between the ichthyofaunas occured in Gondwana and Laurussia and probably was more obvious during the Givetian-early Frasnian than during the late Frasnian-Famennian. This conclusion seems to be corroborated by the distribution of the Tristichopteridae, a group of Sarcopterygians which probably originated and initially evolved in the Laurussian continent, and achieved a wider distribution including Gondwana during the late Frasnian or early Famennian (Ahlberg & Johanson 1997).

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APPENDIX

List of characters summarizing character distribution in *Bothriolepis* from Baltic and NW Russia. **0**, absent; **1**, present; **?**, unknown character state. The characters have been defined for future parsimony analysis as a run of the matrix with the PHYLIP package gave one solution corresponding to a totally pectinated topology. This solution is not retrieved with the same matrix in PAUP which proposed a fully unresolved topology. In agreement with the author, the phylogenetic part is not published as previously envisaged. Abbreviations: **AMD**, anterior median dorsal plate; **AVL**, anterior ventro-lateral plate; **CD5**, dorsal central plate 5; **cit2**, transverse thickening on the visceral surface of AVL; **CV1**, **2**, ventral central plates 1, 2; **La**, lateral plate; **MM1**, **2**, mesial marginal plates 1, 2; **MxL**, mixilateral plate; **Nu**, nuchal plate; **Pmg**, postmarginal plate; **Pn**, paranuchal plate; **Pp**, postpineal plate; **Prl**, prelateral plate; **Prm**, premedian plate; **Sm**, submarginal plate; ***B.***, *Bothriolepis*; ***G.***, *Grossilepis*.

1. AMD in adults broadest across lateral corners, and MxL broadest through its dorsal corner.
2. Lateral corners on AMD appear early in ontogeny.
3. Point contact between Mm1 and CV2 plates of pectoral fin, to separate CV1 from MM2.
4. Axillary foramen longer than high.
5. Pectoral pit-line traced on the CV1 continuing on the CV2.
6. Obtected nuchal area present on Pn.
7. Trifid preorbital recess.
8. Thickened bone edges on orbital margins of Prm and La plates.
9. Long middle pit-line and supraoccipital sensory grooves present.
10. Short Sm plate.
11. Crista transversalis anterior transversely oriented (parallel to cit2) on ventral lamina of AVL.
12. Branch of the infraorbital sensory line diverging on the Prl parallel to the rostral margin of the head-shield.
13. Squarish Nu with convex anterior division of the lateral margin and short postero-lateral corners.
14. CD5 present in distal segment.
15. Pmg of trapezoid rather than of rhomboid shape.
16. Main lateral line canal reaches the posterior margin of the MxL plate.
17. Trunk-armour with pronounced median dorsal crest.
18. Pp orbital margin at the level of lateral corners of the head-shield.
19. Long branch of the infraorbital sensory line diverging on the Prl.
20. Ventro-lateral ridge makes a keel.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
G. tuberculata (Gross, 1941)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. prima Gross, 1942	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. obrutschewi Gross, 1942	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. cellulosa (Pander *in* Keyserling, 1846)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. panderi Lahusen, 1880	1	1	?	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0
B. traudscholdi Jaekel, 1927	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. maxima Gross, 1933	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0
B. evaldi Lyarskaja, 1986	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. leptocheira Traquair, 1893	1	1	1	1	1	1	1	0	1	?	0	0	1	1	1	0	0	0	0	0
B. ornata Eichwald, 1840	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
B. jani Luksevics, 1986	1	1	1	1	?	1	1	1	1	?	1	0	0	0	0	1	0	0	0	0
B. heckeri n. sp.	1	1	?	?	?	?	1	?	?	?	?	0	0	0	0	?	1	1	1	?
B. ciecere Lyarskaja *in* Lyarskaja & Savvaitova, 1974	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1