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ERVĪNS LUKŠEVIČS

Austrumeiropas platformas ziemeļrietumu daļas bruņuzivis (Placodermi, Bothriolepididae)

Zinātniskais vadītājs:

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

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Introduction and acknowledgements

The family Bothriolepididae is the most diverse group of antiarchs represented in the western part of the East European Platform at least by 16 species. The Upper Devonian of the Baltic region and north-western part of Russia is being subdivided mostly by fish data. Bothriolepididae are very important for the correlation of the Frasnian and Famennian non-marine 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 except South America.

W.Gross, E.Kurik, L.Lyarskaya, D.Obruchev, V.Talimaa and others provided lists of agnathans and fishes characteristic for various Devonian beds in the Baltics and north-western part of Russia, described vertebrate assemblages and correlated some strata with the Upper Devonian of other regions. 6 new species have been described from the Main Devonian Field since E.Stensiö's 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 were 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 more complete information on some previously known Frasnian and mostly Famennian fish associations, revision of such poorly known species as *Bothriolepis curonica* Gross, *B.panderi* Lahusen and *B.ornata* Eichw., as well as descriptions of some new species (*B.jani*). 16 taxa of *Bothriolepis* and *Grossilepis* from the Main Devonian Field have been named and described in this manuscript.

The placoderm fish material from Latvia and Lithuania comprises numerous well preserved disarticulated plates as well as complete head shields and fragments of trunk armour. New reconstructions of fish armour are suggested here. During the preparation of this work the main task was to provide descriptions, photos and drawings to illustrate the armour structure of each species as completely as possible. *Bothriolepis* is considerably variable in the shape of individual plates and their overlap patterns as well as in the course of sensory line canals. A separate chapter in this work is dedicated to the investigation of *Bothriolepis* variability using a new statistic method, proposed by Cherepanov (1986).

The largest part of studied and described specimens are housed in the Latvian Museum of Natural History (Riga) and is represented by the collections of L.Lyarskaya, W.Gross, N.Delle, V.Sorokin, J.Upenieks and the author. Besides them specimens from the collections of the Paleontological Institute (Moscow; coll. D.Obruchev, R.Hecker, J.Eglons, N.Krupina, F.Chernyshov), Lithuanian Institute of Geology (Vilnius; coll. V.Talimaa), Mining Museum (St.-Petersburg; coll. H.Helmersen, I.Lahusen, A.Olivieri),

Institute of the Earth Crust (St.-Petersburg; coll. A.Ivanov), Geological Museum of the University of Latvia (Riga; coll. N.Delle, R.Kampe), Natural History Museum (London; coll. P.Egerton, J.Eglons, R.Gross), Royal Scottish Museum (Edinburgh; coll. R.Gross, H.Trautschold, J.V.Rohon) were studied.

The following abbreviations are used to refer to repositories: LDM - Latvian Museum of Natural History (Riga), PIN - Paleontological Institute of the Russian Academy of Sciences (Moscow), LGI - Lithuanian Institute of Geology (Vilnius), GM - Mining Museum (St.-Petersburg), LP - Institute of the Earth Crust (St.-Petersburg), LUGM - Geological Museum of the University of Latvia (Riga), NMH - The Natural History Museum (London), RSM - Royal Scottish Museum (Edinburgh), SMNH - Swedish Museum of Natural History (Stockholm).

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Technique and terminology

Antiarch remains from the Main Devonian Field are usually found as separate plates or fragments of armour and only rarely as whole skeletons (in four localities only). Well preserved complete armour of *Bothriolepis evaldi* Lyarskaja was found by V.Sorokin for the first time and than collected by L.Lyarskaya from an outcrop at the Amula River downstream from Kalnamuiža watermill. Prof. D.Obruchev collected whole specimens of *B.trautscholdi* Jaekel at the Syass 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, Šķēde, Venta Rivers, Lode and Jēkabpils quarries in Latvia, Skaistgiris quarry in Lithuania, Syass, Velikaya and Priksha Rivers in Russia (Leningrad, Novgorod and Pskov regions). 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 Dr. E.Kurik (Lyarskaya, 1981).

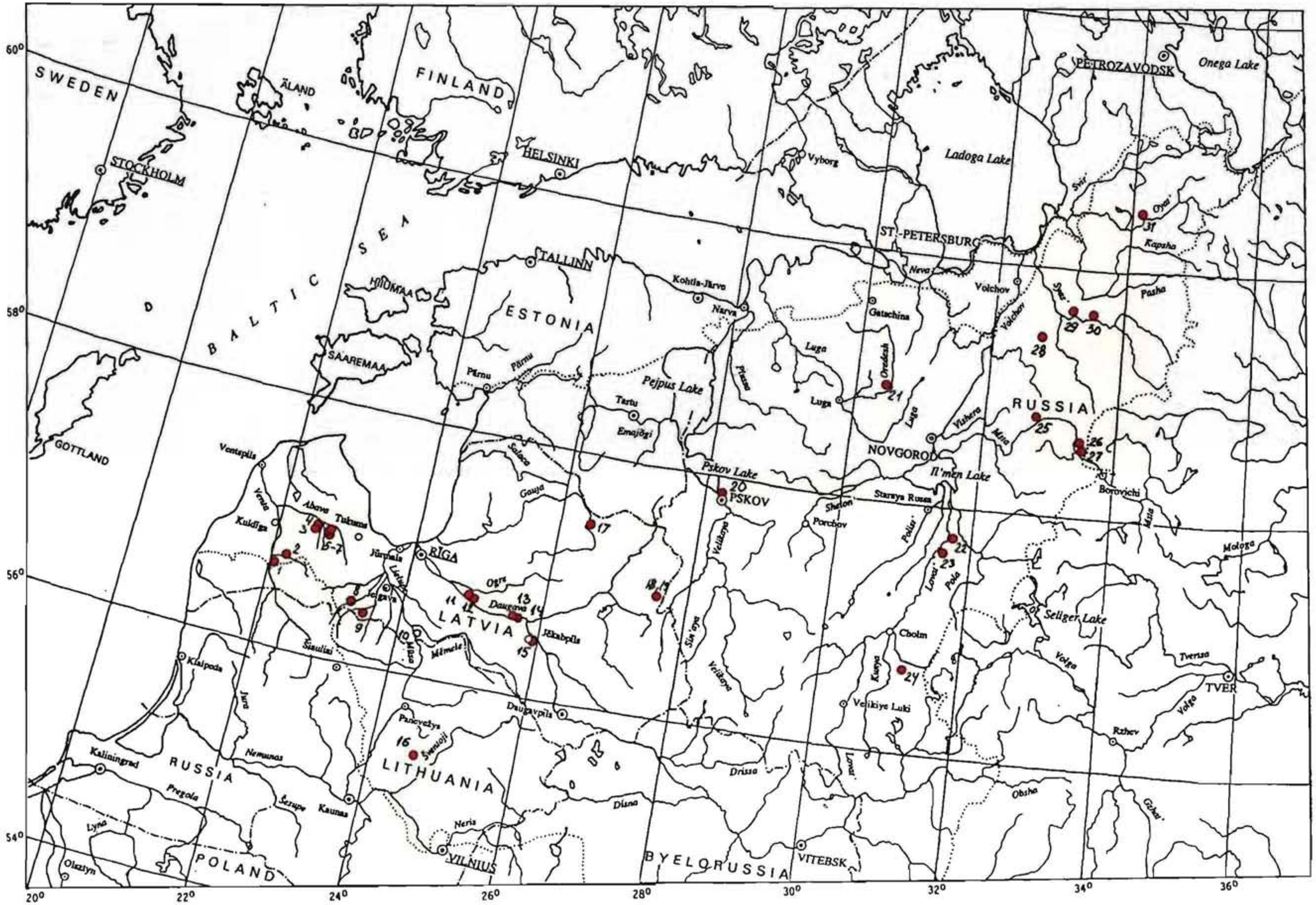
Mounted needles and stomatological equipment were normally used. The chemical methods, such as preparation in 7-10 per cent acetic acid solution, were used in some cases.

Outline drawings were mostly prepared from the specimen photos. The photos in the plates 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. Measurements were taken with vernier calipers usually on original specimens.

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

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

Text-fig.1. Map showing the limits of the Main Devonian Field (dotted line) and some localities (red circles) where studied Bothriolepis material came from. 1 Ketleri, 2 Pavāri, 3 Bienes, 4 Kalnarāji, 5 Kalnamuiža 1, 6 Kalnamuiža 2, 7 Velna Ala, 8 Klūnas, 9 Ķurbes, 10 Ceraukste, 11 Lielvārde, 12 Kaibala, 13 Koknese, 14 Pastamuiža, 15 Jēkabpils, 16 Pelyša, 17 Vidaga, 18 Katleši, 19 Kuprava, 20 Piskovichi, 21 Yam-Tesovo, 22 Kurskoye Gorodishche, 23 Luka, 24 Bilovo, 25 Solodka, 26 Lyubitino, 27 Zarubino, 28 Paluitsa, 29 Montsevo, 30 Stolbovo, 31 Vachukintsy



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HELSINKI
BALTIC SEA
HIIUMAA
SAAREMAA
TALLINN
ESTONIA
Kohtla-Järve
Narva
Pärnu
Tartu
Emajõgi
Pejpus Lake
Pskov Lake
PSKOV
Vyborg
Ladoga Lake
ST.-PETERSBURG
Neva
Gatschina
Luga
Oredezh
Volchov
Svir'
Oyat'
Kapsha
Pasha
PETROZAVODSK
Onega Lake
RUSSIA
NOVGOROD
Il'men Lake
Msta
Vishera
Borovichi
Staraya Russa
Shelon
Porchov
Polist'
Lovat'
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Kunya
Velikiye Luki
Seliger Lake
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TVER
Rzhev
Mologa
Velikaya
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Ventspils
Venta
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RIGA
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Ogre
Daugava
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Panevežys
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Historical account

The generic name *Bothriolepis* was introduced by Eichwald (1840a) during the description of materials collected by H.Helmersen and A.Olivieri. Eichwald mentioned *Holoptychius nobilissimus* Ag. and two new taxa - "*Asterolepis*" and *Bothriolepis ornata* neither illustrating any samples nor indicating precise localities. As noted by Helmersen (Helmersen, 1840; after Karatajūte-Talimaa, 1963), these fish remains were sampled between Ilmen' and Seliger Lakes and at the Msta River, but labels of *Bothriolepis ornata* specimens from A.Olivieri collection preserved in the Mining Museum (Sankt-Petersburg) provide information about a locality at the Priksha River in the vicinities of Borovichi town in the Novgorod region.

In another work published at the same time (Eichwald, 1840b) he mentioned *Asterolepis ornata* and *Bothryolepis prisca* (original transcription) from the sandstones exposed near Ilmen' Lake, *B.prisca* as well from the Priksha River, but again without detailed description of these taxa. Later this author described *B.priscus* from the Middle Devonian deposits at Slavyanka River near Pavlovsk town in the vicinity of Sankt-Petersburg (Eichwald, 1844b). Here Obruchev's opinion (*in* Karatajūte-Talimaa, 1963) is joined to consider that these remains would belong to Coccosteidae.

In his monograph on the Devonian fishes of the Great Britain and Russia L.Agassiz described *Bothriolepis ornatus* Eichw. and *B.favosa* Ag. (Agassiz, 1844-1845) among others. Pl.29, figs.1, 2 shows the remains of *B.ornatus*, as though found by R.Murchison on Priksha River (Agassiz, 1844-1845, p.149). However Andrews (1982) regarded the original drawings for the monograph make possible affirmation that reproduced specimens were collected by Robertson in Elgin and belong to *Bothriolepis gigantea* Traq.; *B.ornata* on the pl.29, figs.3-5 actually are *B.gigantea* from Monachty Hill near Elgin, Scotland (Andrews, 1982). Pl.27, fig.7 and pl.28, fig.12 show large fragments of crossopterygian lower jaws, pl.28, fig.13 and pl.30A, fig.13 show additionally the outer bone surface with tubercular ornamentation corresponding to the jaws mentioned above, which Agassiz referred to as *B.favosa*. Pl.31A shows *B.favosa* from Russia: fig.32 - a crossopterygian operculum (?) from St.-Petersburg region, collected by Keyserling; fig.33 - a bone fragment from Chudovo (probably from Pskov-Chudovo Beds); fig.34 - from Megra (Snezha-Lovat Beds); fig.35 - Prussino (all collected by Murchison). Unfortunately, all specimens illustrated in pl.31A, except fig.32, are small indeterminable pieces of bones with more or less pronounced tubercular ornamentation, but fig.32 shows larger specimen from its visceral surface, that also could not be identified. Thus, Agassiz described most bones of crossopterygian fishes with tubercular ornamentation found in Russia as *B.favosa*. This specific name should be therefore rejected from the list of *Bothriolepis* valid names.

C.Pander described a new antiarch species from the Upper Devonian marls of Latvia as *Pterychthys cellulosa* (Pander: *in* Keyserling, 1846), which was referred by W.Gross to *Bothriolepis* (Gross, 1932). Later Pander in the description of *Asterolepis ornata* reproduced some plates of *Bothriolepis*, and it is possible, that he did not recognize the differences between these two genera (for example, see a picture of the pectoral fin bone, pl.7, fig.23) (Pander, 1857). 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), are actually the remains of *B.trautscholdi* Jaekel (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 the genera, several species of *Asterolepis*, as well as for *Bothriolepis ornata* (Eichwald, 1860). In the pl.56, fig.3 of mentioned monograph, but in the Russian edition (Eichwald, 1861: pl.35, fig.3) he inaccurately traced AMD from Helmersen's collection (specimen GM 116/107) without mentioning the locality. This bone was proposed by Woodward as a type specimen of *B.ornata* (Woodward, 1891). In the same paper Eichwald also suggested, that *B.ornata* was found near Izhma River, Timan (Lower Famennian), near Maryino village at Slavyanka River (Middle Devonian), near Riga and Derpt (now Tartu in Estonia) (Middle Devonian?), as well as near Elgin in Scotland. He also suggested that abundant fish remains from Priksha River belong to *A.ornata.*

Such a list of localities clearly shows that different fishes were grouped in *Asterolepis ornata* by Eichwald. Described specimens # 1/2811 and 1/2812 kept at the Museum of Department of Historical Geology of St.Petersburg University and determined by Eichwald as *B.ornata*, are actually small fragments of *Asterolepis ornata* trunk armour, collected near Burtnieki Lake in Latvia. Following Agassiz Eichwald accepted teeth of *Holoptychius* as belonging to *B.ornata* (Eichwald, 1861, p.451).

In 1880 I.Lahusen erected a new species *B.panderi* to commemorate one of the founders of Russian paleontology (Lahusen, 1880). Unfortunately he did not chose a type specimen and that caused some confusions later on. Pl.1, figs.1,2 show the head shield with articulated anterior part of the trunk armour (GM 1/96) found at Syass River near Montsevo by Pander in 1846. This specimen was reproduced also by D.V.Obruchev (1928; 1947), Stensiö (1948) and proposed as lectotype by Gross (1932). In the pl.2, figs.2-4, Lahusen reproduced the head shield, AMD and PMD collected by Trautschold also at the Syass River. A specimen of the head shield was shown at the pl.4, fig.6 (Gross, 1933) with an indication of the Breslau Museum as a repository (now Wroclaw in Poland). Reproduced specimens (pl.2, fig.2-4; not found neither in Wroclaw, nor in St.-Petersburg: A.Ivanov, pers.comm.) and lectotype of *B.panderi* certainly belong to different species.

At the same time H.Trautschold (1880) provided a detailed description and very superficial reproduction of the abovementioned head shield, as well as corrected the shape of Nu and passing of the central sensory line groove in Lahusen's drawings.

A new period in the study of the Devonian vertebrates and especially antiarchs started in the 1930, with the works of W.Gross in Latvia and Estonia and D.V.Obruchev in Russia. In a short article dated 1928 Obruchev described sclerotic plates of *B.panderi*, using the lectotype GM 1/96 (Obruchev, 1928). 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.

In 1932 W.Gross published a catalogue of fossil antiarchs, provided 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 (Gross, 1932). *Bothriolepis* species from the Main Devonian Field are represented in the catalogue by four taxa - *Bothriolepis ornata* Eichw., *B.cellulosa* (Pander), *B.panderi* Lahusen and *B.maxima* sp.nov.

In 1933 Gross provided more detailed description of all these species. Since Pander had not selected the type specimen of *Pterichthys cellulosa* Gross choose the head-shield from the type locality (pl.IV, fig.15; in the text erroneously mentioned fig.12 reproducing nuchal plate) 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* among the material (for example, mixilateral and nuchal plates, pl.IV, figs.5 and 12 respectively). Later Gross described a new species found together with *B.cellulosa* in Koknese (Kokenhusen), characterized by smaller size and tubercular ornamentation: *B.tuberculata* Gross (1941). In 1933 he presented detailed analysis of similarities and differences in the structure of the pectoral fin in various groups of antiarchs and proposed a new terminology for plates composing the pectoral fin which is being used until now, as well as noted for the first time the presence of two new *Bothriolepis* species in the b-Stufe (Amata Formation sandstones in the modern chart).

Short descriptions of *Bothriolepis prima* Gross, *B.obrutschewi* Gross, *B.spinosa* Gross and *B.curonica* Gross provided by Gross in his fundamental work of 1942 on the fishes of the Baltic Devonian and their stratigraphic significance were based on few remains and wanted complement. Unfortunately due to the political situation in Europe after the Second World War Gross was unable to continue his work on the Baltic material and only a more detailed description of *B.maxima* was supplemented by him to Stensiö's monograph (1948).

Stensiö (1948) reviewed all known species of *Bothriolepis* from Latvia and Russia among others, and also established a new genus *Grossilepis* for *Bothriolepis tuberculata* and

B.spinosa, which differ considerably from other *Bothriolepis* taxa in the shape of the trunk armour plates and tubercular ornamentation. This classic work may be considered as by all means the most complete description of morphology of *Bothriolepis*, however not absolutely accurate in all details.

D.Obruchev in his Atlas of Guide Fossils (Obruchev, 1947) provided short definitions of four species of *Bothriolepis* and reproduced some bones: posterior median dorsal plate 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; posterior median dorsal plate shown by Gross (1933) in the pl.IV, fig.14 and nuchal plate of *B.ornata* collected by R.Hecker at Priksha River.

D.M.S.Watson (1961) supplemented details of morphology of *Bothriolepis panderi* based on the perfectly preserved specimen from Syass River provided to him by Obruchev.

The large collection in the LGI has been the principal source for the detailed descriptions of *Bothriolepis prima* and *B.obrutschewi* that have been made by V.Talimaa (Karatajūte-Talimaa, 1966). She compared these taxa, created reconstructions of the head-shields and trunk-armours of both species for the first time and described two new *Bothriolepis* taxa without giving specific names. Some questions of taphonomy, ecology and phylogeny of the Lower Frasnian *Bothriolepis* from the Baltic have been presented in this work.

Y.Obrucheva provided a relatively schematic reconstruction of *Bothriolepis maxima* armour based mostly on specimen PIN 1491/41 from Nadsnezha Beds, 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 (Obrucheva, 1974).

Investigation of the structure and fish assemblages of Ketleri Formation resulted in establishing of two new species - *Bothriolepis ciecere* Lyarskaja and *B.pavariensis* Lyarskaja (Lyarskaya, Savvaitova, 1974). Lyarskaya claimed that *B.pavariensis* is larger than *B.ciecere* and differs from the latter by wider praemedian plate, shape of the postpineal plate, size and position of external openings of canals for the passage of endolimphatic ducts, shape and position of central sensory line groove branches, shape of anterior median dorsal plate. Unfortunately the description was based on few imperfectly preserved bones. Reexamination of the described and reproduced specimens and additional material collected by the author made possible the suggestion that the abovementioned differences between *B.pavariensis* and *B.ciecere* could be explained mostly by age variation (size of the plates, shape of praemedian, postpineal and anterior median dorsal plates) or individual variations (position of sensory line grooves) which are considerable in *B.ciecere* (Lukševičs, 1991).

In 1986 the list of antiarchs from Latvia was supplemented by two new species of *Bothriolepis*: *B.evaldi* Lyarskaja and *B.jani* Lukševičs (Lyarskaya, 1986; Lukševičs, 1986).

Reexamination of the specimens described by Gross and investigation of materials collected by Lyarskaya, Sorokin and the author made possible the issue of more detailed description and reconstruction of *B.curonica* trunk armour (Lukševičs, 1987). As a result of restudy of *B.ornata* type specimen, collections of Olivieri, Helmersen, Hecker, Talimaa and newly excavated materials it become possible to describe the type species of the genus *Bothriolepis* in more details and analyze its importance for correlation of the Upper Devonian deposits with some distant areas (Lukševičs, 1992).

R.Denison (1978) reviewed all known placoderm fishes, providing a complete list of species, short notes on distribution, morphology and ecology of placoderms including Bothriolepididae. He accounted 46 species of *Bothriolepis*, 2 species of *Grossilepis* and *Hillsaspis gippslandiensis* now referred back to *Bothriolepis* by Young & Gorter (1981), as well as number of unnamed *Bothriolepis* taxa from all over the world. Later the newly discovered *Bothriolepis* specimens were described from Russia (Matukhin et al., 1980; Ivanov & Hozatsky, 1986), Kazakhstan (Malinovskaya, 1977; 1988), Iran (Blieck et al., 1980), Turkey (Janvier, 1980), China (Pan Kiang, 1981; Pan Jiang et al., 1980; 1987; Pan Jiang, 1988), Vietnam (Long et al., 1990), North America (Virginia) (Weem et al., 1981), Australia (Long, 1983; Young, 1987; 1990), Antarctica (Young, 1986; 1988), South Africa (Anderson & al., 1994). G.Young published a number of works on biogeography, morphology and phylogeny of placoderms (1974; 1984a; 1984b; 1986). Some papers were dedicated to the morphology of *Bothriolepis* (Werdelin & Long, 1986), placoderm phylogeny (Janvier & Pan Jiang, 1982; Gardiner, 1984; Goujet, 1984) and ecology of fossil animal assemblages including *Bothriolepis* (Novitskaya et al., 1983; Lukševičs, 1993).

Principles of systematics

There is no widely adopted classification of placoderms (Obruchev, 1964; Miles, 1968; Denison, 1978, 1983; Young, 1984; Goujet & Young, 1995); placoderm groups are being subdivided using strongly differing criteria. Up to now Obruchev's classification (Obruchev, 1964) was usually used in the Russian paleoichthyological papers. According to Obruchev the class Placodermi have been divided into two subclasses: Arthodira including 10 orders and Antiarcha consisting of two orders: Asterolepidida and Remigolepidida (in some works Asterolepiformes and Remigolepiformes) (Karatajūte-Talimaa, 1963, 1966; Malinovskaya, 1977; Lyarskaya, 1981). Subclasses are defined on the basis of differences in the structure of the head-shield, position of orbits and pineal plate, structure of shoulder girdle and pectoral fin, cervical joint and some other features. Most recently the point of view have been accepted that Antiarchi are to be regarded as one of several groups of similar taxonomic range: order (Janvier, 1977; Denison, 1978, 1983), or sister group of Euarthrodira (Young, 1984), Palaeoacanthaspida (Goujet, 1984) or Arthrodira and some other groups of Placodermi, but not all Arthrodira sensu Obruchev (Gardiner, 1984). Recently Goujet and Young (1995) proposed a new scheme of the interrelationships of placoderms. According to the results of their analysis the Antiarcha are placed inbetween the tesserate forms (Acanthothoraci and Rhenanida) and other, more advanced placoderms.

A completely new hypothesis on the relationships of Antiarchi with other vertebrates was suggested by L.Novitskaya (1986). On the basis of a superficial resemblance of the orbital fenestrae of antiarchs and osteostracans, as well as the assumed presence of a nasohypophyseal complex in *Asterolepis ornata*, she claimed, that antiarchs and osteostracans had a similar, actually cyclostome type of ontogeny. Therefore not withstanding number of synapomorphies linking other groups of placoderms with antiarchs the latter group is referred to Agnatha as a sister-group of osteostracans (Novitskaya & Karatajūte-Talimaa, 1989).

Such an interpretation of the interrelationships of antiarchs is based on a number of assumptions, which upon detailed analysis appear rather disputable. The first concerns the homologization of "an orbital window". In osteostracans (*Tremataspis*) a rather simply organized orbital fenestra has arisen as a result of the formation of continuous armour around closely set eye-balls and contains, in addition to them, also a pineal bone (Novitskaya, 1986). The orbital fenestra of antiarchs differs in that its edges are formed by four or five bones: praemedian, paired lateral and postpineal plates, and in bothriolepidids also the nuchal plate. Mesially sclerotic bones, surraunding the eye-ball, are bordered by pineal and rostral plates both bearing overlap areas for the sclerotic bones. The eye-balls are surrounded in a similar way in some other placoderm groups, for example in Palaeacanthaspida. In *Romundina* (Orvig, 1975) and *Kimaspis* (Mark-Kurik, 1973) the orbits mesially are limited by praemedian and rostral plates, in *Brindabellaspis* (Young, 1980) by rostropineal and preorbital plates. The eyes in *Romundina* and *Kimaspis* were dorsolaterally directed, in *Brindabellaspis* they were situated more dorsally, and in antiarchs the eyes are set close together on the dorsal surface of the head; this is possible to explain by adaptation to a benthic style of life of detritophagous fish, not presenting high requirements to the photoreceptors. The orbits becoming closely spaced, the rostral and pineal plates sharing the orbits have decreased in width, resulting in compactness of structures connected with the eye-balls. As to the telencephalon, its position below diencephalon, similarly to osteostracans and lampreys, has been interpreted by Novitskaya only as probable.

Nostrils in antiarchs and osteostracans open on the dorsal surface of a head, in the middle between the eyes. However the similarity between the two groups ends here. In antiarchs paired nostrils opens anteriorly from the rostral plate; a similar position on the head shield is shown by the closely spaced nostrils in palaeacanthaspids *Romundina*, *Kimaspis* and *Radotina*. The Rhenanids *Asterosteus*, *Gemuendina* and *Jagorina* also have closely set dorsal nostrils (Denison, 1978). In osteostracans the unpaired nasohypophyseal opening lies not in the orbital fenestra, but in the bottom of the circumnasal pit (Novitskaya, 1986).

Novitskaya 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 material on *Asterolepis ornata* (LDM 60/48: articulated trunk-armour and head-shield and LDM 60/61: part of the head-shield, both of excellent preservation; Lode quarry) reveals no evidence of such a canal. The slight pit between the praemedian and rostral plates in described specimen is probably a misinterpreted preparation mark. The praenasal wall of the rostral plate is closely fitted to the lower part of the vertically directed posterior wall of the Prm, leaving no place for a canal.

A new interpretation of the situation of the nasal sacs also is in contradiction to the presence of an outer hypophyseal opening in *Asterolepis*. Novitskaya following Lyarskaya (1981) considers fenestrae in the rostral plate as outer nasal openings (nostrils) and places the nasal sacs behind the rostral plate. In this case there is empty space in front of the rostral plate; nostrils opens forward instead of dorsally, as in other antiarchs; and the only possible location for the telencephalon is beneath the diencephalon. I suggest that the nasal sacs in *Asterolepis* are situated behind the Prm plate in two pits on the posterior wall of this plate, posteriorly bounded by the rostral plate. These pits were recognised also by Lyarskaya (1981). Consequently, the nasal sacs were placed some distance from telencephalon (that means the presence of the more or less long olphactory ducts) and opened dorsally. Fenestrae on both sides of the intranasal wall of the rostral plate were, probably, filled by perichondral cartilage pierced by olphactory ducts. A similar situation is observed in *Romundina* (Ørvig, 1975; Pl.5, figs.1-5), in which perichondral ossification on the rostral plate is well preserved. In *Romundina* and *Brindabellaspis* the hypophyseal opening lies on the parasphenoid (Ørvig, 1975; Young, 1980). In antiarchs the endocranium is not ossified, so there is no direct evidence of the position of the hypophyseal opening. However the similarities of *Romundina* and other Palaeoacanthaspida with antiarchs is one more argument against the suggested presence of a nasohypophyseal complex in *Asterolepis*.

At the same time Novitskaya mentions some rather important features, shared by antiarchs and other Gnathostomata. Regarding the significance of the operculum, she considers it as an autapomorphic structure. Another feature is the presence of primitive, but nevertheless real jaw elements, including jaw ossifications, palato-quadrate and Meckelian cartilage. Novitskaya claims that the presence of these jaw elements is not incompatible with the exception of antiarchs from the Gnathostomata, and means only that the occurrence of primitive jaws could happened in main branches of ancient vertebrates more than once (Novitskaya, Karatajūte-Talimaa, 1989). However this is obviously in contradiction with the principle of parsimony. In the case of adoption of Novitskaya' point of view we would have to consider that not only jaws and opercular bones, but also trunk-armour consisting of well homologized plates have arisen in different stems of vertebrates independently.

Antiarchs were subdivided into orders Asterolepidida or Asterolepiformes and Remigolepidida or Remigolepiformes on the basis of different structure of the pectoral fin armour and presence or absence of the mixilateral plate (Karatajūte-Talimaa, 1963; Obruchev, 1964; Malinovskaya, 1977; Lyarskaya, 1981). Obruchev included into Asterolepiformes the families Pterichthyidae, Asterolepididae, Bothriolepididae, Lepadolepididae and Sinolepididae, and Karatajūte-Talimaa the families Asterolepididae, Bothriolepididae, Grossaspididae and Sinolepididae in which the pectoral appendage possess the distal joint and a complex mixilateral plate is present. *Remigolepis* is a genus with the pectoral appendage lacking the distal joint and with two separate lateral plates in the trunk-armour: posterior dorsal lateral plate and posterior lateral plate. This is the only representative of Remigolepiformes. Nevertheless some Asterolepiformes have two only partly fused PDL and PL - *Gerdalepis jesseni* from Eifelian of Germany (Friman, 1982) and *Byssacanthus dilatatus* from the upper part of the Middle Devonian of the Main Devonain Field (Karatajūte-Talimaa, 1959), but *Stegolepis jugata* from Kazakhstan has two separate plates (Malinovskaya, 1973). Gross (1965) pointed out that the absence of the distal joint in the *Remigolepis* pectoral fin could be secondary. Discoveries of abnormal pectoral fins lacking the distal joint in *Asterolepis* are additional evidence for a proposed attribution of *Remigolepis* to Asterolepiformes (Gross, 1965).

Remigolepis closely resembles *Asterolepis* and shares such common features as narrow lateral plates, position of the posterior pit-line on the nuchal and paranuchal plates, shape of praemedial plate with the median notch on the anterior margin, absence of the median ridge on the visceral surface of the anterior and posterior median dorsal plates, shape of pineal plate, position of postmarginal plate on the posterior margin of the head-shield (Lyarskaya, 1981; Stensiö, 1931; Lukševičs, 1991b).

Taking into account all the aforesaid points, classifications which unite asterolepids and bothriolepids could be accepted. Miles (1968) divided the antiarchs into suborders Asterolepidoidei, Bothriolepidoidei and Yunnanolepidoidei. Denison (1978) considered yunnanolepids as belonging to the family Bothriolepididae, and additionelly accepted two more families: Asterolepididae and Sinolepididae. Young and Gorter (1981) provided a new precised definition for bothriolepidoids and asterolepidoids, based on the cladistic analysis of the distribution of features in these antiarchs. They claimed that the exclusion of the Nu from the orbital fenestra by the Pp plate in *Microbrachius* and *Sinolepis* indicates asterolepidoid rather than bothriolepidoid affinities. The subdivision of the family Pterichthyodidae into two subfamilies Pterichthyinae and Gerdalepidinae (Hemmings, 1978) was rejected as not based on strong evidence. Janvier and Pan Jiang (1982), following Miles, regard *Yunnanolepis* as a very primitive and separate genus, characterized by absence of processus brachialis, and refered it to a separate order. The other antiarchs are united into group Euantiarcha (which probably corresponds to a superorder) including orders Sinolepidida, Bothriolepidida and Asterolepidida. The presence of elongated Pp and Nu in *Sinolepis* is mentioned as a feature distinguishing it from *Bothriolepis* and *Asterolepis*. The grouping of asterolepids with bothriolepids is based on several features: shape and proportions of the La plate, presence of the preorbital recess in *Bothriolepis*, position of the Pmg plate (lateral in *Bothriolepis* and posterior in *Asterolepis*), position of the sensory line canals on the head shield, position and contacts of plates of the pectoral appendage (Janvier & Pan Jiang, 1982).

G.Young (1984a) also supports such a scheme, suggesting four groups in the antiarch cladogram (suborder-family range): yuannanolepids, sinolepids, asterolepidoids and bothriolepidoids, uniting the three latter into euantiarch group. Young regarded *Yunnanolepis*, *Zhanjilepis* and *Qujinolepis* as yunnanolepids; *Phymolepis* probably also belongs to this group. Sinolepids include *Sinolepis* and *Xichonolepis*. Bothriolepidoids are the genera *Bothriolepis, Grossilepis, Hyrcanaspis*, as well as the more separate *Dianolepis, Microbrachius* and *Wudinolepis*. Young regarded *Asterolepis, Remigolepis, Pambulaspis* and the sister-group of genera *Pterichthyodes, Byssacanthus, Stegolepis, Sherbonaspis, Gerdalepis, Grossaspis* and *Lepadolepis* as belonging to the asterolepidoids. The synapomorphies of asterolepidoids and bothriolepidoids, as Young claims, are the following: in bothriolepidoids (1) PVL and PL are fused or replaced forming a single plate;

(2) MxL overlaps AMD by most part of their common suture; (3) AMD with broad anterior margin; (4) Sm is unpaired; (5) presence of the posterior oblique cephalic pitline (central sensory line groove). Asterolepidoid synapomorphies are: (1) short obstantic margin facing posteriorly; (2) Pmg extended posterolaterally; (3) suborbital and orbital fenestrae are incorporated the preorbital depression; (4) AMD have no the anterior ventral pit and process; (5) suborbital plates meet in the midline.

Later Young (1988) referred *Bothriolepis verrucosa* Young from the Antarctic to the new genus *Monarolepis*. The new genera and species from the Middle Devonian of Australia *Wurungulepis denisoni* and *Nawagiaspis wadeae* were referred to pterichthyodidae and bothriolepididae respectively (Young, 1990).

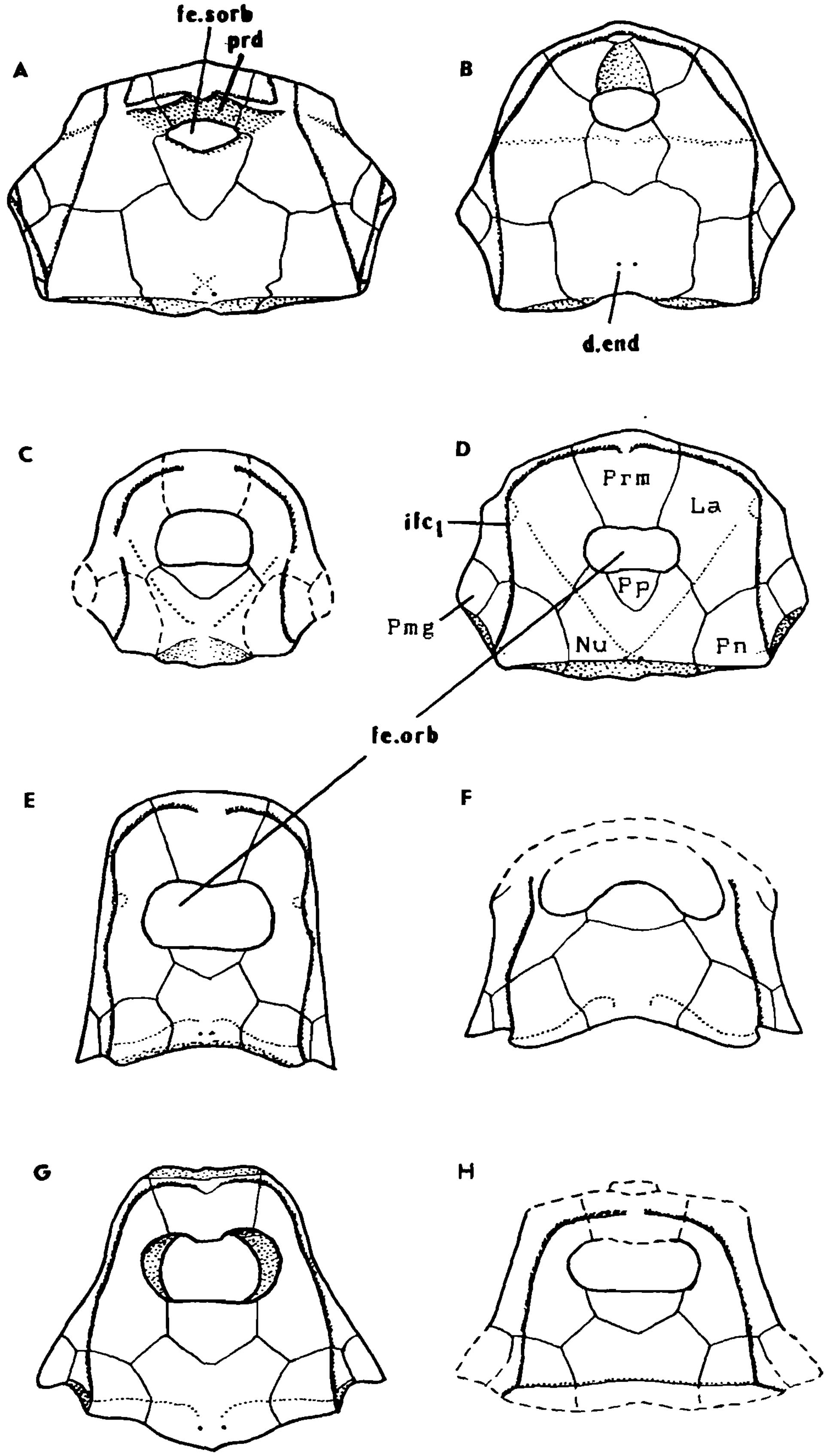
Zhang Guorui (1984) introduced the new antiarch order Procondylolepiformes, including the new family Procondylolepidae. Then Pan et al. (1987) referred the family Procondylolepidae to Euantiarcha. Thon Zong & Janvier (1990) noted that Procondylolepis from China is closely related or similar to *Chuchinolepis* from Vietnam; both are characterized by a weakly developed primitive processus brachialis. So they referred Procondylolepis to the family Chuchinolepidae. Tong-Dzuy & Janvier (1990) described several new species and genus from the Lower Devonian of Vietnam: two species of *Yunnanolepis*, *Chuchinolepis dongmoensis*, *Vanchinolepis bacboensis*; the latter was referred to sinolepids.

Zhang Guorui & Young (1992) described a new bothriolepidoid antiarch *Luquanolepis pileos* from the Early Devonian of China, as well as analysed the distribution of several characters within 13 genera, producing four cladograms of possible bothriolepidoid interrelationsships.

Panteleyev (1993) described a new species of *Sherbonaspis* and a new antiarch, which is, in his opinion, of uncertain affinities: *Asperaspis carinata* with a set of unusual features from the Middle Devonian of Central Kazakhstan. The short and high trunk-shield with a high crest, very short anterior margin of the AMD, short obstantic margin in *Asperaspis carinata* are the features characteristic for Pterichthyodidae. The paired semilunar plate is known also in *Gerdalepis*(Denison, 1978).

Adding the scheme proposed by Young (1984a) by recently described taxa it is possible to suggest the following classification (see below). The new genera *Vietnamaspis* and *Briagalepis* from Vietnam, described by Long et al. (1990), *Jiangxilepis* from China (Zhang & Liu, 1991), *Tenizolepis* from Kazakhstan (Malinovskaya, 1977), *Kirgisolepis*

Text-fig.2. Head-shields of representatives of some antiarch families. A, *Yunnanolepis* (Zhang, 1978). B, *Sinolepis* (Liu et P'an, 1958; Long, 1983). C. *Dianolepis* (Chang, 1965; Denison, 1978). D, *Bothriolepis* (Stensiö, 1948). E, *Byssacanthus*, young exemplar (Karatajūte-Talimaa, 1959). F, *Gerdalepis* (Gross, 1941b). G, *Asterolepis* (Karatajūte-Talimaa, 1963). H, *Remigolepis* (Pan et al., 1987).


A
fe.sorb
prd
B
d.end
C
D
Prm
La
ifc1
Pp
Pmg
Nu
Pn
fe.orb
E
F
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H

from Kirgizia (Panteleyev, 1992) are also included here. All of them were referred by the authors to the family Bothriolepididae. Nevertheless *Tenizolepis* and *Kirgišolepis* are characterized by some features distinguishing them from *Bothriolepis* and resembling that of *Dianolepis*: Pp plate is broad and make contact with the La plate; the relatively short pectoral appendages are not reaching the posterior margin of the trunk-shield; Cd_1 have a common suture with Cd_2. I propose to place both genera into Dianolepididae on the base of these characters.

Class **PLACODERMI**

Superorder ANTIARCHA

Order YUNNANOLEPIFORMES Zhang Guorui, 1978

Family 1 YUNNANOLEPIDIDAE Miles, 1968

Yunnanolepis, Zhanjilepis, Phymolepis (?)

Order EUANTIARCHA Janvier et Pan, 1982

Suborder **Procondylolepidoidei** Zhang, 1984

Family 2 CHUCHINOLEPIDAE K.J.Chang, 1978

Chuchinolepis, *Procondylolepis*

Suborder **Sinolepidoidei** Long, 1983

Family 3 SINOLEPIDIDAE Liu et P'an, 1958

Sinolepis, Xichonolepis, Vanchienolepis

Suborder **Bothriolepidoidei** Miles, 1968

Family 4 DIANOLEPIDIDAE Long, 1983

Dianolepis, Jiangxilepis, Kirgisolepis, Tenizolepis

Family 5 BOTHRIOLEPIDIDAE Cope, 1886

Bothriolepis, Briagalepis, Grossilepis, Monarolepis, Vietnamaspis

INCERTAE FAMILIAE

Hohsienolepis, Luquanolepis, Microbrachius, Nawagiaspis, Taeniolepis, Wudinolepis (?)

Suborder **Asterolepidoidei** Miles, 1968

Family 6 PTERICHTHYODIDAE Stensio, 1948

Pterichthyodes, Asperaspis, Byssacanthus, Grossaspis, Gerdalepis, Hyrcanaspis (?), Hunanolepis, Lepadolepis, Stegolepis, Sherbonaspis, Wurungulepis

Family 7 ASTEROLEPIDIDAE Traquair, 1888

Asterolepis, Pambulaspis, Remigolepis

Systematic descriptions

Euantiarcha Janvier et Pan, 1982
Bothriolepidoidei Miles, 1968
Bothriolepididae Cope, 1886

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

Bothriolepis Eichwald, 1840

T y p e s p e c i e s: *Bothriolepis ornata* Eichwald, 1840.
D i a g n o s i s. 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 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
Plate 1, Figs. A-E

Bothriolepis prima : Gross, 1942, S.415-416, Abb.6.
Bothriolepis prima Gross: Karatajūte-Talimaa, 1966, p.192-202; text-figs.1-4, 5.1; pl.I-VI; VII, figs.1-8.

H o l o t y p e. Anterior median dorsal plate (Gross, 1942, Abb.6A).
D i a g n o s i s. Small *Bothriolepis* with a median dorsal armour length reaching 50 mm. Breadth/length index of the head-shield of 140-150. Weakly convex rostral margin is slightly shorter than the posterior margin. The obtected nuchal area is present only on Nu. The orbital fenestra is relatively large. Lateral division of Pn is narrow. Nu bears posterior process. Dorsal wall of the trunk-armour broad and high in its anterior part and relatively narrow in posterior part. 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, breadth/length index of 101. PMD of moderate breadth with narrow anterior margin. Posterior margin is usually rounded. Dorsal lamina of ADL relatively narrow, dorsal and lateral laminae enclosing an angle about 122-128^{o}. Angle between the dorsal and lateral walls on MxL is sharper: about 112^{o}. Lateral and ventral walls enclosing an angle about 109^{o} 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. Ventral lamina of AVL and PVL more than twice as long as it is broad. Lateral lamina of PVL is 1.7 times as long as it is high. Ventral wall of the trunk-shield is relatively narrow, breadth/length index of 46, with relatively broad anterior part and narrow posterior part. MV is small. Proximal segment of the pectoral appendage of moderate length, 3.8-4.5 times as long as it is broad. Lateral and mesial spines on the proximal segment are separate and relatively long. Distal segment is relatively short, 3.8 times as long as it is broad. Ornamentation is always reticulate in small and moderately large individuals. Central part of the dorsal and ventral walls bears almost smooth ornament in small individuals. In rather large individuals ornamentation of the head-shield and dorsal wall of the trunk-armour become more tuberculate. Sensory line groove system is well developed. Pit-line groove crossing the dorso-lateral ridge on the MxL is always present.

M a t e r i a l. 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: disarticulated plates. 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.

L o c a l i t i e s. Daugava River near Pastamuiža at the vicinity of Koknese, Latvia. Pelyša River, Lithuania. Yam-Tesovo at Oredezh River, Russia.

H o r i z o n. Upper Devonian, Lower Frasnian, lower part of the Amata Formation of Latvia; Staritsa Beds of Russia.

R e m a r k s. *Bothriolepis prima* is well described by Karatajūte-Talimaa (1966) and the description is not repeated here.

Bothriolepis obrutschewi Gross, 1942

Plate 2

Bothriolepis obrutschewi: Gross, 1942, S.416-418, Abb.7.
Bothriolepis obrutschewi Gross: Karatajūte-Talimaa, 1966, p.202-216, text-fig.5, fig.2; 6, figs.1,2; 7; 9; 10; 12; pl.VII, fig.8; IX-XXIII; XXIV, figs.1-8.

H o l o t y p e. Mixilateral plate (Gross, 1942, Abb.7B).

D i a g n o s i s. *Bothriolepis* of moderate size with a median dorsal armour length reaching 80-85 mm. Breadth/length index of the head-shield about 127. Anterior part of the head-shield is relatively flat, posterior part arched. The weakly convex rostral margin is slightly shorter than the posterior margin. Orbital margin of Prm is stright, without nasal notches. Rostral margin of Prm weakly convex. Anterior and posterior margins of the orbital fenestra are straight. Pp with straight or gently convex anterior margin. Nu is arched, with long obtected nuchal area presented only on Nu. Lateral division of Pn is narrow. Pmg is elongated. Dorsal wall of the trunk-armour low and relatively narrow, breadth/length index of 86. Tergal angle weakly defined, situated in anterior part of the middle third of AMD. Median dorsal ridge on AMD is present only in very small individuals, it is more clearly defined in PMD. Shape and proportions of AMD are variable, AMD relatively broad, breadth/length index about 99.5. Anterior division of the lateral margin is more than twice longer than the posterior division. Overlap area for MxL often is of *Remigolepis*-type. PMD of moderate breadth. Dorsal lamina of ADL relatively narrow, 2.5 times as long as it is broad. Dorsal and lateral laminae enclosing an angle about 121°. Angle between the dorsal and lateral walls on MxL about 114°. Dorsal lamina of MxL 1.5-1.7 times as long as it is broad. Lateral and ventral walls enclosing an angle about 119° on PVL. Ventral wall of the trunk-shield is of moderate breadth. Ventral lamina of AVL is 1.8-2 times as long as it is broad. Ventral lamina of PVL is more than twice as long as it is broad. Lateral lamina of PVL is relatively high with well defined dorsal corner. MV is small. Sm relatively broad. 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 a 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. Distal segment bears longitudinal ridges.

M a t e r i a l. 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-shield with proximal segments of the pectoral fin and head-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 43/585-671, 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.
L o c a l i t i e s. Pastamuiža, Latvia. Pelyša River; Paroveja borehole, 49.65-49.75 m deep, Lithuania. Piskovichi, Russia.
H o r i z o n. Upper Devonian, Lower Frasnian, upper part of Amata Formation of Latvia; uppermost part of Šventoji Formation of Lithuania.
D e s c r i p t i o n. The head-shield in small individuals has a large orbital fenestra and short anterior division. In larger individuals the head-shield is moderately broad with breadth/length index about 123-131, 127 on the average. In general the head-shield of *B.obrutschewi* is narrower than that of *B.cellulosa* and *B.prima*. It is relatively flat anteriorly and vaulted posteriorly. The rostral margin of the head-shield is convex, sometimes bearing the rostral angle; usually it is slightly shorter than the posterior margin, which is almost straight. 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 plate. The orbital fenestra is relatively large, moderately long and narrow with a breadth/length index about 173. Preorbital recess (prh) is distinctly trifid with rounded lateral and a pointed median division.

The praemedian plate is moderately broad, the breadth/length index changing from about 134 in smallest individuals with the Prm 6 mm long to 94-95 in well-grown individuals with 16-18 mm long Prm. It is broadest at the infraorbital sensory groove. The rostral margin is usually straight or slightly convex. The rostral angle (ac) is present only on the two large Prm. The orbital margin is straight, rarely gently convex, it is 1.4-1.8 times shorter than the rostral margin. The infraorbital sensory groove crosses the plate in its anterior part.

The lateral plate is moderately broad with the length/breadth index 130-173, 148 on the average. The rostral margin is of moderate breadth and almost straight, the antero-median and antero-lateral corners are well defined. The infraorbital sensory line groove crosses the plate in its anterior part not far from the orbital and lateral margins. The central sensory line groove (csl) usually finishes at the level of the orbital margin of the orbital fenestra. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined. The visceral plate surface shows the normal features. The antero-lateral corner of otico-occipital depression (pr.po) extends 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 plate and prelateral notch.

The postpineal plate is broad in small individuals and of moderate breadth in maturity. As in other species the anterior margin is strongly convex in small specimens and became almost straight with increasing size.

The nuchal plate is relatively broad with a length/breadth 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 posterior process (mppr). The central sensory line groove is clearly distinct. Specimen LGI 5/2248 shows unusual feature: the Pp plate is broad, making contact with the La plate and excluding the Nu plate from the contact with the orbital fenestra.

The paranuchal plate is of moderate breadth, length/breadth index about 74-97, 84 on the average. 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 postmarginal plate is moderately broad with the lateral margin slightly longer than the median margin.

The submarginal (extralateral) plate is known from one specimen, LGI 5/2230. It is relatively long with a length/breadth index of about 250. The dorsal margin has a prominent anterodorsal 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 (n.la) is rather deep separating the plate into a short thick anterior division and more thin posterior division. There is a groove (gr.sc) 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 is moderately broad, breadth/length index 86, weakly arched anteriorly and more arched posteriorly. 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 subcaudal 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 anterior median dorsal plate is moderately broad, breadth/length index about 89-98, 94 on the average. 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 and often is as long as the posterior margin or less. 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 tergal angle (dma) is situated posteriorly the anterior third of the plate and is weakly marked. 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 (dlg_1) 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 (dlg_2) oblique dorsal sensory line grooves usually are well defined. In some cases the posterior oblique dorsal sensory line grooves are shortened or interrupted (LGI 5/5/2639).

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) and in a posterior part also by the postlevator cristae. The anterior ventral pit (pt_1) and the median ventral ridge (mvr) are well defined.

The posterior median dorsal plate is moderately broad, breadth/length 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*. 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. The median ventral ridge and median ventral groove with short posterior ventral pit (pt_2) 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 anterior dorsal lateral plate is relatively broad, the dorsal lamina is 1.9-2.1 times as long as it is broad and it's breadth 1.2-1.5 times exceeds height of the lateral lamina. Dorsal and lateral laminae of the plate enclosing an angle of about 121° on the average. 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.

The mixilateral plate is moderately broad. The dorsal lamina of the plate is 1.4-1.6 times as long as it is broad. Dorsal and lateral laminae enclosing an angle about 114°. The lateral lamina is moderately high. The dorso-lateral ridge is well defined. The posterior oblique sensory line groove (dlg_2) terminates close to the lateral margin, in some distance from the dorso-ventral pit-line groove crossing the dorso-lateral ridge. The overlap area for the AMD is often restricted to half the length of the antero-dorsal margin (LGI 5/2485, 5/2490, 5/2491), as in *Remigolepis* (Stensiö, 1931).

The anterior ventral lateral plate is of moderate breadth, the ventral lamina is 1.6-1.8 times 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 elongated in shape. The visceral surface of the AVL shows the high transverse anterior crista (cit_1) running almost mesially subparallel to the gently defined low and broad transverse thickening (cit_2).

The posterior ventral lateral plate 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 and long, 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*; the ventral lamina is 1.2-1.3 times as broad as the lateral lamina high. The angle between laminae is about 119^{o}. The ventro-lateral ridge (vlr) is well defined.

The median ventral plate is typically developed.

The pectoral fin is represented by many disarticulated bones, and five specimens showing articulated plates of the proximal segment. There are fourteen examples of the distal segments or their fragments. The proximal segment is relatively long, 4-4.5 times as long as it is broad. The Cd_1 is of moderate size with length/breadth index varying from 2.7 to 3.1 (2.8 on the average). The Cv_1 is slightly longer than the Cd_1 and have the length/breadth index about 3.1-3.4 (3.2 on the average). The Ml_2 is 4.2-4.4 times as long as it is broad. The distal segment shows only Cd_3, it is long and relatively narrow with the length/breadth index about 5-5.4. Both segments bear prominent lateral and mesial spines. On the proximal segment the isolated mesial spines are large and high. The lateral spines are fused in their base forming well defined crest.

The ornamentation is of tubercular type in general. It consists of coarse tubercles and short vermiculated ridges of fused tubercles on the head-shield. The short radially arranged ridges are developed along the margins of the La and Nu plates. The network of anastomosing ridges, which are broken into short ridges could be sometimes seen on the posterior part of the Prm plate. The ornament on the Sm plate 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. 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 Cd_1 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 Ml_2 and Cv_1. 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.

D i s c u s s i o n. *B.obrutschewi* resembles *B.prima* by several features, but differs from *B.prima* in its (1) narrower head-shield; (2) relatively broader dorsal and ventral walls of the trunk-armour; (3) relatively longer subcaudal division of the PVL; (4) smaller orbital fenestra; (5) shape of the postlevator cristae on the visceral surface of the AMD plate; (6) proportions of the ADL; (7) more strongly defined tubercular ornament; (8) development of the central sensory line groove (csl) and the anterior oblique dorsal sensory line groove (dlg_1) 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 plate; (3) shape of the postnuchal ornamented corner of the ADL plate; (4) narrower ventral wall of the trunk-shield; (5) shorter proximal segment of the pectoral fin.

B.obrutschewi resembles *B.panderi* Lahusen by the ornamentation, but differs from it in its (1) smaller size; (2) shape and proportions of the head shield; (3) proportions of the lateral division of the Pn plate, which is narrower in *B.obrutschewi*; (4) broader AMD; (5) relatively narrower anterior margin of the AMD; (6) relatively shorter pectoral fin.

B.obrutschewi can be distinguished from *B.cellulosa* (Pander) (Gross, 1941), other Lower Frasnian *Bothriolepis* representative from the Main Devonian Field mostly by its smaller size and ornamentation.

Bothriolepis cellulosa (Pander), 1846

Pterichthys cellulosa: Pander in Keyserling, 1846, S.292.
Bothriolepis retinata: Hoffman, S.293,297, Abb.14,15; Taf.24, Fig.4.
Bothriolepis retinata Hoffman: Gross, 1931, S.58.
Bothriolepis retinata Hoffman: Stensiö, 1931, p.11.
Bothriolepis cellulosa (Pander): Gross, 1932, S.24 (in part).
Bothriolepis cellulosa (Pander): Gross, 1933, S.36-39, Abb.36-39; Taf.4, Fig.1, 9, 10, 12, 15; Taf.5, Fig.12 (in part).
Bothriolepis cellulosa (Pander): Gross, 1941, S.4-32, Abb.1-8, 9A-C,10A,11A-E,12-24; Taf.1-6; Taf.7, Fig.1-3, 5; Taf.8-13; Taf.14, Fig.2-4; Taf.15; Taf.16, Fig.1-4; Taf.17, Fig.1 (in part).
Bothriolepis cellulosa (Pander): Obruchev, 1947, p.204, text-fig.66 (non Pl.LV, fig.4).
Bothriolepis cellulosa (Pander): Stensiö, 1948, pp.405-424, text-figs. 14, 23E-G, 24C, 26C, 28B, 31C-D, 35D-E, 39C, 41C, 45D-E, 50C, 53C, 218-228.
Bothriolepis cellulosa (Pander): Karatajūte-Talimaa, 1966, text-fig.6, fig.3; text-figs.8,11,13.

H o l o t y p e. The head-shield (Gross, 1933, Taf.4, Fig.15).
D i a g n o s i s. *Bothriolepis* of moderate size with a median dorsal armour length of at least 190 mm. Head-shield is relatively broad, breadth/length index of 128-146, 138 on the average, and comparatively flat in its praeorbital division. Anterior margin of the head-shield is considerably shorter than posterior margin, slightly convex and rounded with a rostral angle. Praeorbital recess is of simple type. Praemedian plate is broad, posterior margin is much shorter than the anterior margin. Pineal plate broader than long or about as broad as long. Nuchal plate is broad, length/breadth index of 65-81, 70 on the average. Lateral division of paranuchal plate 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 plate. 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, breadth/length index 83-94, 89 on the average. PMD comparatively broad with breadth/length index about 82-112, 96 on the average; anterior margin is broad, posterior corner obtuse or rounded off. Dorsal lamina of ADL plate about twice as long as broad; lateral lamina about two and a third times as long as high. Dorsal lamina of MxL plate from about 1.7 to 1.9 times as long as broad; lateral lamina is comparatively high: from about 2 to 2.2 times as long as high. Lateral lamina of AVL plate conceivably a little more than three times as long as high. Ventral lamina of

AVL from about one and a half times to about twice as long as broad. PVL plate with a somewhat well-pronounced dorsal corner; lateral lamina about two and a half times as long as high; ventral lamina from two and a half to about two and three fourths times as long as broad. Pectoral fin fairly robust. Proximal segment is moderately long, 3.5 to 4 times as longs as broad. Lateral spines of proximal segment comparatively short. Medial spines fairly strongly developed and independent; the median spines situated on the Cd_1 plate and on the adjacent parts of the Mm_2 plate pointing dorsally. Cd_1 plate about 2.5-3 times as long as broad. Cv_1 plate from about 2.7 to 3.4 times as long as broad. Ml_2 plate 4.2-5.6 times as long as broad. 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 large 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.

M a t e r i a l. 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; NMH P.17807, 17810, 17813, 17814, 17818, 17826, 17828, 17829, 17836, 17837: Nu, AMD, 2 PMD, 4 MxL, AVL, 4 fin bones; RSM 1964.26.41 (SMNH P.3275): impression of the AMD and AVL.

L o c a l i t i e s. The type locality is an outcrop of dolomites, dolomite marls and clays at the right bank of Daugava River near Koknese. The other material comes from Pastamuiža, Latvia; outcrop at the right bank of Velikaya River in Pskov near Piskovichi, Russia.

H o r i z o n. The Lower Frasnian Pļaviņas Regional Substage, Snetnaya Gora and Sēlija Beds (Pskov Beds in eastern part of the Main Devonian Field).

R e m a r k s. *Bothriolepis cellulosa* is well described by W.Gross (1941) and E.Stensiö (1948) and its description is not repeated here.

Bothriolepis panderi Lahusen, 1880

Plate 1, Fig. F; Text-figs. 7 G, H

Bothriolepis panderi: Lahusen, 1880, S. 137, Taf.1, figs. 1-5; Taf.2, fig. 1 (non figs. 2-4).
Bothriolepis panderi Lahusen: Obruchev, 1928, p.142-144, Pl.IX, fig.9.
Bothriolepis panderi Lahusen: Gross, 1932, S. 25 (partim).
Bothriolepis panderi Lahusen: Obruchev, 1947, p. 204, Pl. LV, fig. 5.
Bothriolepis panderi Lahusen: Stensiö, 1948, p. 424; text-fig. 230, 232.

L e c t o t y p e. The complete head shield and anterior part of the trunk armour MM 1/96.
D i a g n o s i s. Somewhat large *Bothriolepis* with a median dorsal armour length of at least 125 mm. Breadth/length index of the head shield is 147. The rostral margin is convex, much shorter than the posterior margin. The orbital fenestra is relatively small, short and broad, with a breadth/length index 180. Praemedian plate is relatively broad, breadth/length index is 100; the slightly convex orbital margin is much shorter than the rostral margin. The rostral plate is twice as broad as it is long and bears deep and short nasal notch. The 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. Nuchal plate relatively broad, length/breadth index of 61. The postmarginal plate is longer than broad with lateral margin much longer than median margin. Trunk-armour is relatively broad, with somewhat elevated dorsal wall. AMD is moderately broad, breadth/length index about 71. The anterior margin is moderately broad, 1.5 times 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. The Cd_1 is of moderate size with length/breadth index about 2.6. The ornamentation consists of tubercles and short vermiculated ridges both on the head-shield and the trunk-armour.
M a t e r i a l. SMNH P.3387, Cd_1; MM 2/96, 3/96, fragments of the pectoral fin; LDM 63/337, AVL, 63/338, ADL.
L o c a l i t i e s. Outcrop at the right bank of Syas' River along Montsevo village, Russia.
H o r i z o n. The Lower Frasnian Snetnaya Gora Beds.
D e s c r i p t i o n. *Bothriolepis panderi* have 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 head shield is relatively broad, breadth/ length index is 147 in lectotype. It is comparatively flat in its anterior part and

slightly vaulted in the posterior part. The rostral margin is convex, much shorter than the posterior margin. It seems to be relatively narrower than that in *B.cellulosa*. The orbital fenestra is relatively small, short and broad, with a breadth/length index 180.

Praemedian plate is relatively broad, breadth/length index is 100. It is broadest at the infraorbital sensory groove or rostral margin. The orbital margin is slightly convex, it is much shorter than the rostral margin. The orbital margin seems to be devoid the nasal notch. The infraorbital sensory groove crosses the plate in its anterior part.

The lateral plates on both sides of the lectotype are crushed and therefore not seem to 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 (csl) is finished slightly anteriorly the level of middle of the orbital fenestra length. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined.

The rostral plate is much broader and shorter than in *B.canadensis*. It is twice as broad as it is long and bears deep and short nasal notch.

The pineal plate is relatively broad, breadth slightly exceeds a length. The postero-lateral corners are well defined. The anterior and lateral margins are concave, the posterior margin is almost straight. Outer surface of the plate is pierced by the pineal opening.

The postpineal plate is long and broad, length/breadth index is 156. The anterior margin is slightly convex.

The nuchal plate is deficient posteriorly and therefore its proportions cannot be calculated with full accuracy. However, it seems to be relatively broad with a length/breadth index of 61. The plate is broadest across the lateral corners. The anterior division of the lateral margin is concave and a little shorter than the posterior division. There are short supraoccipital grooves (socc), which terminate little in front of the obtected nuchal area at the rather large external openings for the endolymphatic ducts ($d.end_2$).

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

The postmarginal plate is longer than broad with the lateral margin much longer than the median margin.

The three sclerotic plates (pl. 1, fig. F) in most features are similar to that of *B.canadensis* (Stensio, 1948; text-fig.21).

The trunk armour is relatively broad. The dorsal wall 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 median dorsal plate is moderately broad, estimated breadth/length index about 71. The anterior margin is weakly convex. It is moderately broad and 1.5 times shorter than the maximum breadth of the plate. The antero-lateral and lateral corners are rounded, the postlevator processes are strongly defined. 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 the ADL and MxL are normally developed as usually in *Bothriolepis*. The posterior (dlg_2) oblique dorsal sensory line grooves are well defined.

The dorsal lamina of the anterior dorsal lateral plate is relatively narrow and long. The dorso-lateral ridge (dlr) is well defined. The postnuchal ornamented corner (pnoa) is massive, long and broad.

The anterior ventral lateral plate is of moderate breadth. The subcephalic division is short. The anterior lateral corner of subcephalic division is situated in the middle between the median and lateral margins; it is developed into a short broad process. The visceral surface of the AVL shows the high transverse anterior crista (cit_1) running antero-mesially and low and broad transverse thickening (cit_2) running more mesially.

The pectoral fin is represented by articulated plates of the proximal segment. The proximal segment 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 set. The Cd_1 is of moderate size with length/breadth index about 2.6.

The ornamentation consists of tubercles and short vermiculated ridges with few anastomoses both on the head-shield and trunk armour.

R e m a r k s. Lahusen (1880) erected a new species *B.panderi* for the remains of bothriolepids from the several localities at the Syas' River. Reexamination of the lectotype and additional materials allowed to distinguish at least two separate species: one from the locality Montsevo and other from near Stolbovo village, as well as from some other localities. Gross (1932) proposed the head-shield MM 1/96 as a lectotype of *B.panderi*. Jaekel (1927) illustrated the skull roof from the Stolbovo locality as belonging to the other species *B.trautscholdi*. Later Gross (1933) suggested *B.trautscholdi* to be synonymous to *B.panderi*.

D i s c u s s i o n. *Bothriolepis panderi* resembles *B.cellulosa* (Pander) in certain aspects, but differs from it by some features. *B.panderi* differs from *B.cellulosa* in (1) the shape and proportions of the Prm; (2) the shape of the Pi; (3) the shape and forward extension of the Pn; (4) the slender proximal segment of the pectoral fin; (5) character of coarser ornamentation with tubercles and anastomosing ridges.

The species *B.panderi* and *B.taylori* Miles 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 angle 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 Cd_1. *B.paradoxa* (Ag.) 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.trautscholdi* see the description of the latter).

Bothriolepis trautscholdi Jaekel, 1927

Plates 3-6; Text-figs. 3-6, 7 A-F

Bothriolepis panderi: Lahusen, 1880, S. 137, Taf. 2, figs. 2-4.
Bothriolepis panderi Lahusen: Trautschold, 1880, S. 172 (fig.).
Bothriolepis trautscholdi: Jaekel, 1927, S.869, 932, Abb.21, 60.
Bothriolepis panderi Lahusen: Gross, 1932, S.25 (partim).
Bothriolepis panderi Lahusen: Gross, 1933, S. 39,40, Taf. 4, fig. 6; Abb.21.
Bothriolepis panderi Lahusen: Gross, 1941, Abb. 10 B,C, 11 G,H, 26 H-K, 27 D,E.
Bothriolepis panderi Lahusen: Stensiö, 1948, p. 424; text-fig. 229A, 231 (non text-fig.230).
Bothriolepis panderi Lahusen: Watson, 1961, text-fig.1.
Bothriolepis panderi Lahusen: Obruchev, 1964, Pl. 6, fig. 6.

T y p e s p e c i m e n. Jaekel (1927) illustrated the head shield of a proposed new species *Bothriolepis trautscholdi*, collected by Trautschold (1880, shown also by Gross in 1933) at the Syas' River not far from Stolbovo village (Russia) and mentioned to be kept at the Museum of Breslau (now Wroclav in Poland). The collection of Trautschold is partly remained at this museum, but the specimen shown by Jaekel is probably lost (pers.comm. A.Ivanov). Therefore I propose here the head shield PIN 330/33, collected by J.Eglons in 1937 at the Syas' River near Stolbovo village and shown by Obruchev (1964) in the Plate 6, fig.6, as a neotype of *Bothriolepis trautscholdi* Jaekel (this species was named as *Bothriolepis tremdscholdi* n.sp. in Abb.21 and *B.traudscholdi* Jkl. in Abb.60 of Jaekkel's paper; both are regarding to be misprintings of the name *B.trautscholdi*, which was used by Gross (1933).

D i a g n o s i s. Rather large *Bothriolepis* with a median dorsal armour length of at least 140 mm. Head shield of moderate width, breadth/length index 133, with strongly convex anterior margin shorter that posterior margin. Orbital fenestra large and long. Preorbital recess is of simple type. Lateral pit of the La plate is small and deep. Nuchal plate is moderately broad with breadth/length index of about 81; it is broadest across the postero-lateral corners. AMD is moderately broad, breadth/length index about 94. The anterior margin 1.9 times shorter than the maximum width of the plate. Median dorsal ridge weakly developed and practically absent in large individuals. PMD is relatively broad with breadth/length index about 104. Postnuchal ornamented angle of the ADL is sharp, usually long and narrow. AVL is comparatively broad with moderately long subcephalic division. Proximal segment of the pectoral fin is slender, about five 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 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.

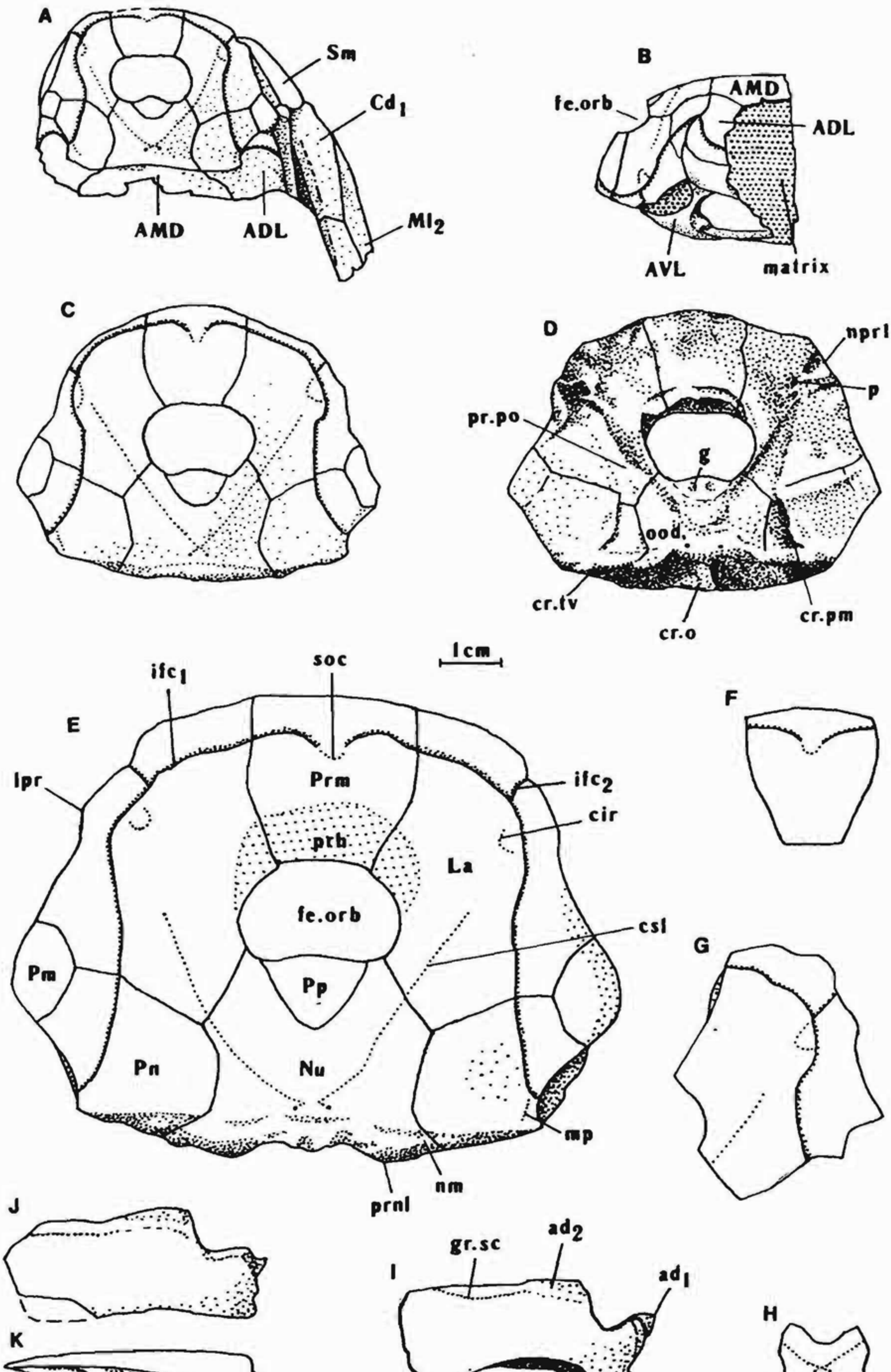
M a t e r i a l. PIN 330/39, 41-75, 77-98, 100-107, 110-128, 29/1, 2, articulated head shields and disarticulated plates of the skull roof and trunk armour; PIN 2917/41-46, articulated head shields and anterior divisions of the trunk armour; LDM 63/1-33, 35-51, 53-230, 241-306, LP 14/1-5, disarticulated plates of the skull roof and trunk armour; LP 14/6, articulated plates of the dorsal trunk armour; NMH P.34465, sandstone block with 20 bones, including articulated head-shield; RSM 1902.72.4, AMD plate, 1902.72.6, PMD plate. 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.

L o c a l i t i e s. The type locality is outcrop exposing the dark-coloured sandstones with thin layers of clayey siltstones, multicolored marls and clays at the right bank of Syas' River near Stolbovo village. Other material comes from the outcrops at Syas' River near Yukhora village, Russia, and exposure of the dolomites at the left bank of Gauja River not far from Vidaga village, Latvia.

H o r i z o n. All material from Russia came from the Frasnian Dubnik Formation and specimens from Latvia, locality at Gauja River, came from the Altovo Member of the Daugava Formation.

D e s c r i p t i o n. This species is well represented at the locality at the right bank of Syas' River near Stolbovo village by many disarticulated plates, as well as some articulated skulls and trunk shields, which are usually well preserved. Almost all the specimens from Vidaga site at Gauja River are incomplete and usually deformed, in many cases preserved only as

Text-fig.3. *Bothriolepis trautscholdi* Jaekel. A, head-shield, anterior part of AMD, both ADL, right AVL and proximal segment of the pectoral fin PIN 2917/43 in dorsal view. B, head-shield, anterior part of AMD, left ADL, AVL, Cd_1 and Cv_1 PIN 2917/45 in lateral view. C, D, head-shield PIN 330/117 in dorsal view and visceral view. E, head-shield PIN 330/113 in dorsal view. F, Prm plate PIN 330/118. G, La plate LDM 63/131. H, Nu plate LDM 63/149. I-K, submarginal plates. I, PIN 330/116 in lateral view. J, K, PIN 330/114 in lateral and ventral view. Stolbovo, right bank of Syas' River, Russia. Dubnik Formation.



A
Sm
Cd1
AMD
ADL
Ml2
B
AMD
fe.orb
ADL
AVL
matrix
C
D
npr1
p
pr.po
g
ood.
cr.tv
cr.o
cr.pm
1cm
E
soc
ifc1
ifc2
lpr
Prm
cir
prb
La
fe.orb
csl
Pm
Pp
Pn
Nu
mp
nm
prnl
F
G
J
K
I
gr.sc
ad2
ad1
H

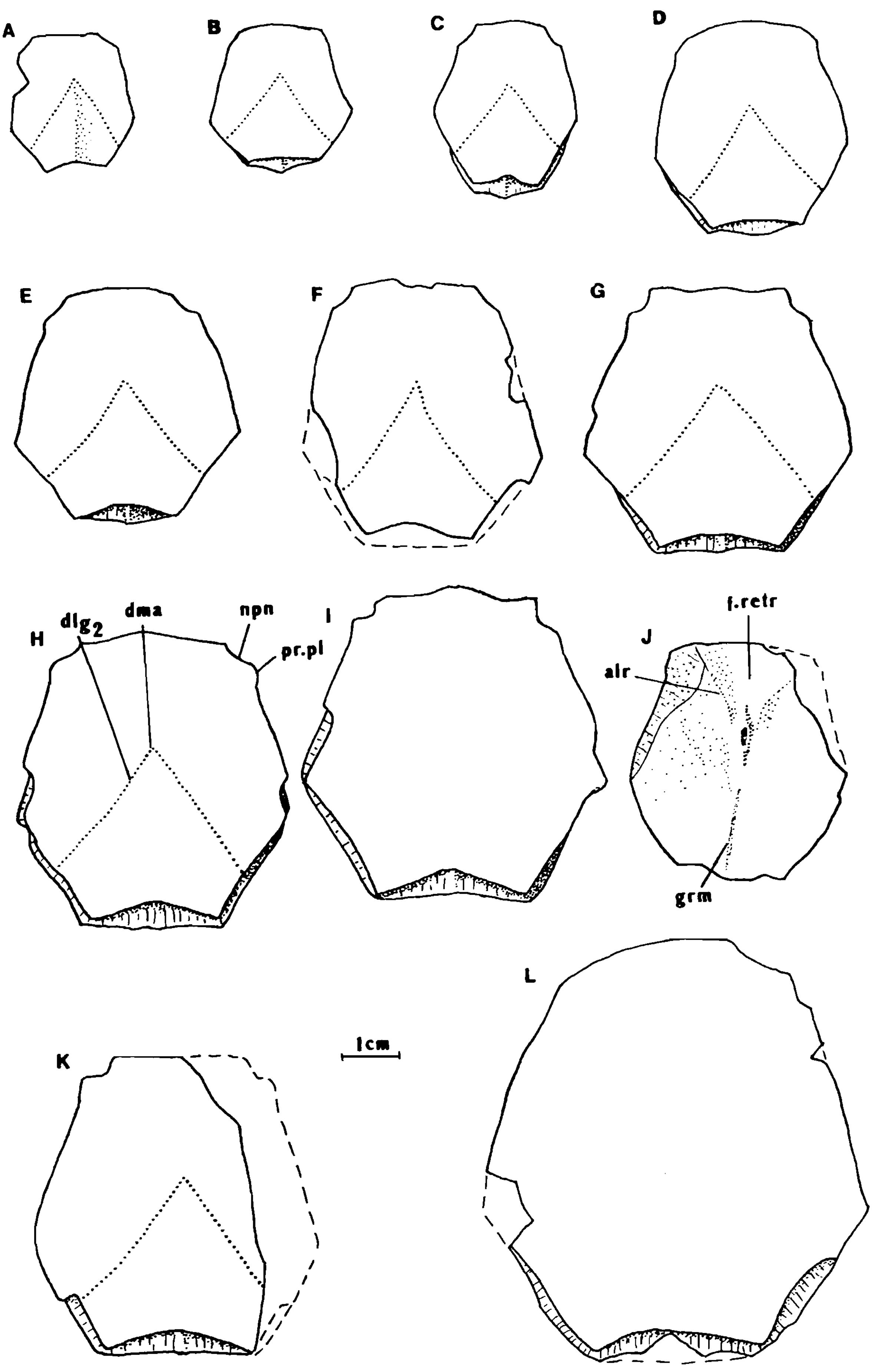
an impressions. Most are from small or well-grown individuals of moderate size, but there are also some quite large specimens. The length of the head shield reaches about 75 mm, the dorsal length of the trunk armour is estimated at least about 140 mm. The head shield is of moderate width, breadth/length index is of 130-140, 133 on the average. The head shield is strongly vaulted both rostrocaudally and transversely in small individuals and became more flat in well-grown individuals. The rostral margin is strongly convex, shorter than the posterior margin, which is weakly convex or almost straight. There are well defined anterolateral corners (alc) and the deep prelateral notch (nprl). The obtected nuchal area (nm) is of moderate width, broadest on the Nu plate, usually with well defined lateral and median processes. The orbital fenestra is moderately large, comparatively long, with a breadth/length index about 150-167, 156 on the average. Preorbital recess (prh) is of simple type.

The visceral skull surface 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 plate's posterior margin. The transverse lateral groove (tlg) is moderately broad and clearly defined. The lateral pit (p) is situated more close to a prelateral notch than to the orbital edge of La plate, it is small but rather deep. The median occipital crista (cr.o) is slightly defined, often it consists from several radially situated 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 plate is low.

The praemedian plate is relatively broad, breadth/length 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 infraorbital sensory groove crosses the plate in its anterior part. The anterior section of the supraorbital sensory line (soc) usually is clearly defined.

The lateral plate is moderately broad with length/breadth index of 130-143, 134 on the average. The rostral margin is of moderate breadth and 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

Text-fig.4. *Bothriolepis trautscholdi* Jaekel. A-L, AMD plates, A-I, K, L, in dorsal view, J, in visceral view. A, LDM 63/18. B, LDM 63/24. C, LDM 63/7. D, LDM 63/41. E, PIN 330/52. F, LDM 63/8. G, PIN 330/55. H, LDM 63/37. I, PIN 330/53. J, LDM 63/13. K, LDM 71/34. L, LDM 63/30. A-J, L, Stolbovo, right bank of Syas' River, Russia. Dubnik Formation. K, Vidaga, left bank of Gauja River, Latvia. Altovo Member of the Daugava Formation.


A
B
C
D
E
F
G
H
dlg2
dma
npn
pr.pl
I
J
f.retr
alr
grm
K
1cm
L

line groove (csl) usually is finished at the level of the anterior margin of the orbital fenestra. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined.

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

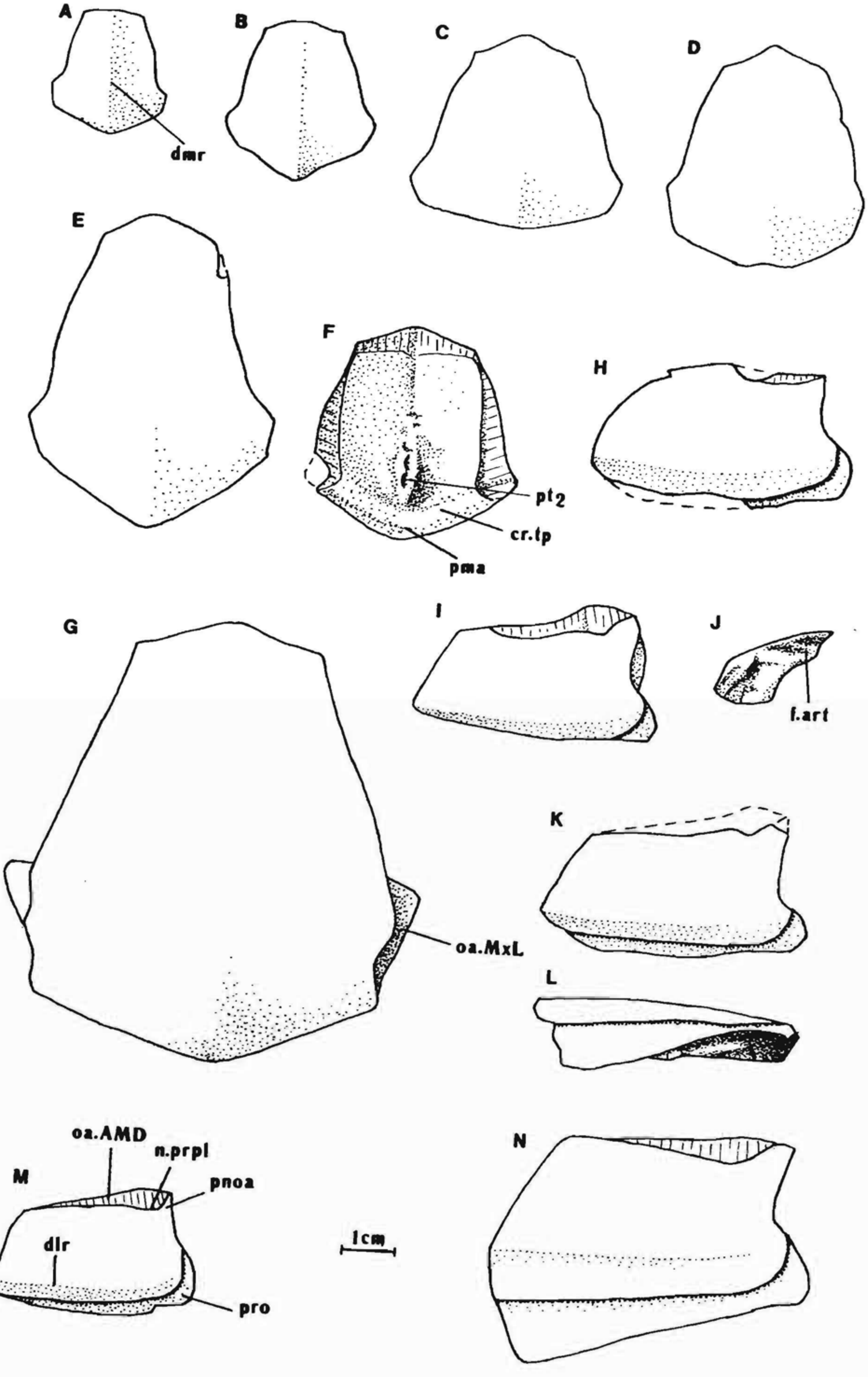
The nuchal plate (text-fig. 3) is moderately broad with a length/breadth index 71-90, 81 on the average. The plate is broadest across the postero-lateral corners. The anterior division of the lateral margin usually is almost straight and well shorter than the posterior division. The shape of the posterior 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 ($d.end_2$). Postorbital crista (cr.pto) on the visceral surface is moderately high.

The paranuchal plate is of moderately long, length/breadth 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 postmarginal plate is relatively broad with lateral margins longer than the median margins.

The submarginal (extralateral) plate (pl. 4, figs. K-M; text-figs. 3 I-K) is comparatively long with length/breadth index about 220-270. The dorsal margin has a prominent anterodorsal process (ad_1) 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 (n.la) is rather deep separating the plate into a short thick anterior division and more thin posterior division. The specimen PIN 330/116 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* and *B.macphersoni* and has the character of a sensory groove.

Text-fig.5. *Bothriolepis trautscholdi* Jaekel. A-G, PMD plates, A-E, G, in dorsal view, F, in visceral view. A, LDM 63/76. B, LDM 63/71. C, LDM 63/65. D, PIN 330/47. E, PIN 330/48. F, PIN 330/50. G, LDM 63/58. H-N, ADL plates. H, PIN 330/86 in dorsal view. I, J, PIN 330/98 in dorsal and anterior view. K, L, PIN 330/87 in dorsal and lateral view. M, LDM 63/98 in dorsal view. N, LDM 71/45 in dorsal view, somewhat flattened. A-M, Stolbovo, right bank of Syas River, Russia. Dubnik Formation. N, Vidaga, left bank of Gauja River, Latvia. Altovo Member of the Daugava Formation.


A
B
C
D
dmr
E
F
H
pt2
cr.tp
pma
G
I
J
f.art
K
oa.MxL
L
M
oa.AMD
n.prpl
pnoa
dlr
pro
1cm
N

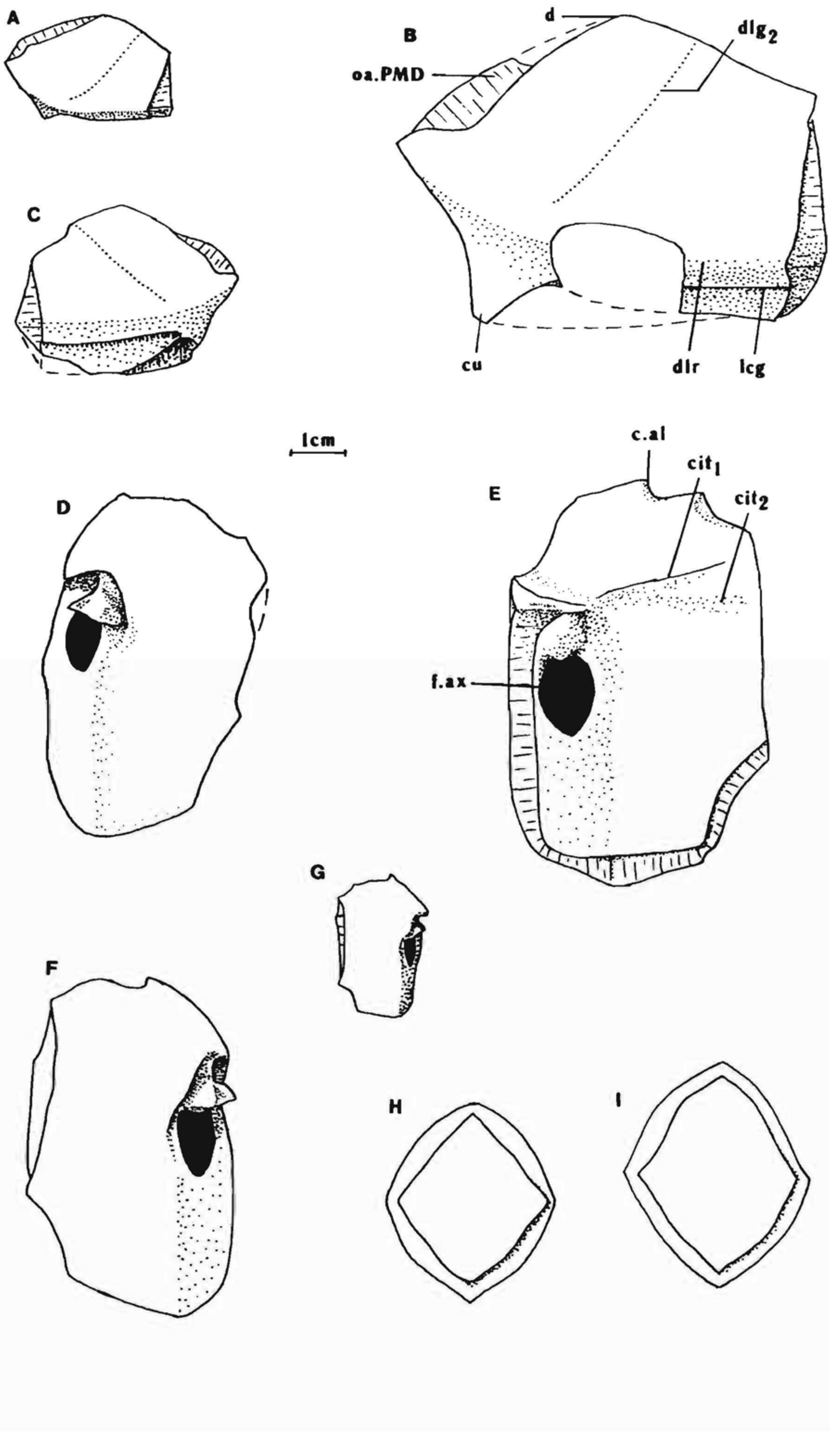
The trunk armour in individuals of moderate size is known from a large amount of disarticulated plates and several anterior parts of the articulated armours, sometimes with articulated pectoral fins, in small individuals.

The trunk-armour in individuals of small size as it is remained in specimens PIN 2917/41-46, is moderately broad, breadth/length 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 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 anterior median dorsal plate (pl. 5; text-fig. 4) is moderately broad, breadth/length index varying from 84 to 105, 94 on the average. The anterior margin is generally convex, sometimes somewhat wavelike in shape, relatively long, less than twice (1.9 on the average) shorter than the maximum breadth. The anterior margin is usually 1.1 times 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 times 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 the 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 (dlg_1) is gently defined only in smallest specimen LDM 63/17 which is 17 mm long. The posterior oblique dorsal sensory line groove (dlg_2) is clearly defined also on the plates of very large individuals. Specimen LDM 63/18 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 and 63/8 sutural connection of AMD with MxL is of *Remigolepis* type. The antero-lateral margin in LDM 63/37 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 (text-fig. 4 J) 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*.

Text-fig.6. *Bothriolepis trautscholdi* Jaekel. A-C, MxL plates. A, LDM 63/85. B, LDM 63/82. C, PIN 330/99. D-G, AVL plates. D, PIN 330/64 in ventral view. E, LDM 63/108 in visceral view. F, LDM 63/107 in ventral view. G, LDM 63/109 in ventral view. I, J, MV plates in ventral view. I, LDM 63/122. J, LDM 63/123. Stolbovo, right bank of Syas' River, Russia. Dubnik Formation.


A
B
C
D
E
F
G
H
I
d
dlg2
oa.PMD
cu
dlr
lcg
1cm
c.al
cit1
cit2
f.ax

The posterior median dorsal plate (pl. 6, figs. A-C; text-figs. 5 A-G) is usually moderately broad, sometimes very broad (LDM 63/65, text-fig. 5 C), breadth/length index varies from 94 to 112, 104 on the average. It 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 angle. The posterior margin usually has rounded, sometimes concave or pointed posterior median angle. The posterolateral angles (plc) are quite distinct. The lateral margins of the plate generally overlapping the mixilateral plate, but there are narrow areas along the lateral process of the PMD plate overlapped by the MxL plate.

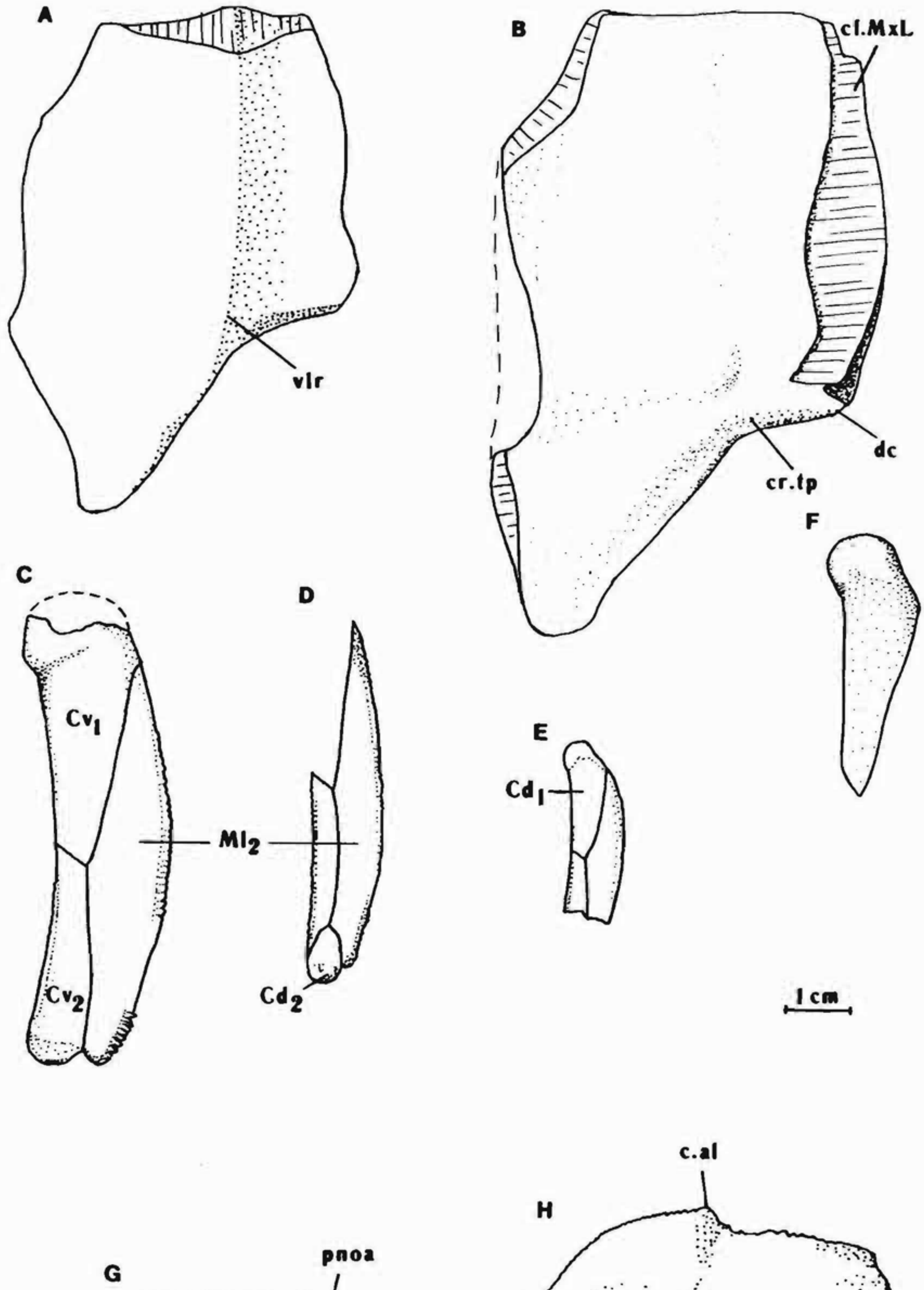
On the visceral surface (text-fig. 5 F) the ventral median groove (grm) is clearly shown also in small specimens, the ventral median ridge (mvr) is low with shallow posterior ventral pit, which is situated in posterior half of the plate. Posterior marginal area (pma) is relatively short.

The anterior dorsal lateral plate (pl. 6, figs. E-J; text-figs. 5 H-N) 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 3 times as long as it is deep. The dorso-lateral ridge is well marked in the posterior part of the plate. The postnuchal ornamented angle (pnoa) is sharp, usually long and narrow, resembling that of *B.ciecere*; in large specimens it is more broad. Notch behind it is poorly formed. Groove of the main lateral line passes the posterior margin of the plate more close to the dorso-lateral ridge. The dorsal margin of the plate bears an overlap area for the anterior median dorsal plate usually along the whole of its length, but in specimens PIN 330/86 (pl. 6, fig. F) and 330/98 (pl. 6, fig. I) the ADL plate overlaps the AMD plate 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).

The mixilateral plate (pl. 6, fig. D; text-figs. 6 A-C) has a comparatively low lateral

Text-fig.7. A-F, *Bothriolepis trautscholdi* Jaekel. A, B, PVL plates. 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, Cv_1 plate LDM 63/158 in ventral view. Stolbovo, right bank of Syas' River, Russia. Dubnik Formation.

G, H, *Bothriolepis panderi* Lahusen. G, fragment of the ADL plate LDM 63/337 in dorsal view. H, anterior part of the AVL plate LDM 63/338 in visceral view. Montsevo, right bank of Syas' River, Russia. Snetnaya Gora Beds.


A
B
cl.MxL
vlr
dc
cr.tp
F
C
D
Cv1
E
Cd1
Ml2
Cv2
Cd2
1 cm
c.al
H
G
pnoa
pbr
cit1

lamina which is more than three times as long as it is deep, and a relatively broad dorsal lamina about 1.6 - 1.7 times as long as it is broad. The anterior margin concave or wavy. Dorsal and lateral laminae meet at an angle of about 113^{o}. Dorsolateral ridge is well marked, in large specimens it is rounded. Overlap area for the AMD in specimen PIN 330/94 is restricted to half the length of the antero-dorsal margin, as in *Remigolepis*.

The anterior ventral lateral plate (text-figs. 6 E-G) is comparatively broad, the ventral lamina is 1.5-1.8 times as long as it is broad. The subcephalic division is moderately long and comprises 20-25 per cent 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 (cit_1) running antero-mesially very close to the broad transverse thickening (cit_2).

The posterior ventral lateral plate (text-figs. 7 A, 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 per cent of the total PVL plate length. The lateral lamina is moderately high, 1.8-2 times long as it is high. The ventral lamina 1.2-1.3 times 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 (text-figs. 7 C-E). 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 Cd_1 is of moderate size with length/breadth index varying from 2.6 to 3.1 (2.8 on the average). The Cv_1 is relatively more elongated and have the length/breadth index about 2.8-3.6 (3.2 on the average). The Ml_2 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 plates. The ornament on the Sm plate 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 Cd_1 and dorsal lamina of the Ml_2 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.

R e m a r k s. *Bothriolepis trautscholdi* was shown by Jaekel (1927) as a new species which differs from *B.panderi*, but did not provide its description. Gross (1933) mentioned *B.trautscholdi* as a synonymous to *B.panderi*, but without any further comments. I suggest that there are several differences between these two species, described below.

D i s c u s s i o n. *Bothriolepis trautscholdi* resembles *B.panderi* by several features: (1) the general shape of the head-shield; (2) proportions of the Pn and Pmg plates; (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 plate; (7) proportions of the slender pectoral fin. Nevertheless *B.trautscholdi* differs considerably from *B.panderi* in its (1) larger size; (2) comparatively narrower head-shield; (3) more vaulted anterior part of the head-shield; (4) larger and longer orbital fenestra; (5) shape and proportions of the Prm and Nu plates; (6) more anterior extent of the central sensory line groove; (7) more broad AMD plate; (8) shorter anterior margin of the AMD; (9) shape of the postnuchal ornamented angle of the ADL plate; (10) longer subcephalic division of the AVL plate.

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

Bothriolepis maxima Gross, 1933

Bothriolepis maxima: Gross, 1932, S.25 (nomen nudum).

Bothriolepis maxima: Gross, 1933, S.41-43; Abb.22, 23; Taf.III, Fig.2; Taf.IV, Figs.3,4; Taf.V, Figs.1,7,11,14.

Bothriolepis maxima: Gross, 1940, Abb.14E.

Bothriolepis maxima: Gross, 1941, S.62; Abb.44A-D; Taf.XXIX, Figs.1-4.

Bothriolepis maxima: Gross, 1942, S.418; Abb.8.

Bothriolepis maxima Gross: Obruchev, 1947, p.204, Pl.LV, fig.1.

Bothriolepis maxima: Gross in Stensiö, 1948, p.432-462; text-figs.24D, 26E, 49, 52, 233-246.

Bothriolepis maxima Gross: Ye.D.Obrucheva, 1974, p.60, fig.1.

H o l o t y p e. The head-shield f124 Geologisch-Paläontologischen Institut und Museum der Universität Berlin (Gross, 1933, Taf.5, Fig.14).

D i a g n o s i s. *Bothriolepis maxima* is the largest known *Bothriolepis*. Median dorsal length of the armour reaches more than 50 cm. Head-shield is short and broad, breadth/length index is about 137-156, 145 on the average, with almost flat praeorbital region. Anterior margin is slightly shorter than posterior margin, it is gently convex, in the middle sometimes with a rounded rostral angle. Processus obstans is relatively short. Prm plate is usually with nasal notches. Both branches of the infraorbital sensory groove meet close together in the middle. Praeorbital recess of trifid type. La plate is broad. Pp plate is relatively long with an almost straight anterior margin. Nu plate is comparatively broad and short, with the length/breadth index of about 57-69, 61 on the average. Outer opening of the endolymphatic ducts are closely set and small. Lateral division of the Pn plate is relatively narrow. Pm plate is slightly longer than broad. Mental plate is 2 times as long as it is high. Trunk armour is relatively low with a moderately high dorsal wall. Dorso-lateral ridges are gently defined and rounded in their anterior part, and dorsal median ridge is weakly developed and practically absent in large individuals. Tergal angle is situated in the foremost part of the middle third of the AMD plate. Ventro-lateral ridges are rounded. AMD plate is about as long as it is broad, with breadth/length index 86-107, 97 on the average. Anterior margin is narrow, more than twice as long as the plate is broad. External postlevator processes are well developed. Ventral median ridge on the visceral surface is well defined and extends well far posteriorly. Postlevator thickenings are weakly defined. PMD is usually broader than it is long with breadth/length index about 96-117, 107 on the average; anterior margin is of moderate breadth, posterior corner rounded off. Dorsal lamina of ADL plate about twice as long as broad, relatively narrow posteriorly the well defined pronounced postnuchal angle; lateral lamina from about three to three and two thirds times as long as high. Dorsal lamina of MxL plate is comparatively broad, from about 1.5 to 1.6 times as long as broad; lateral lamina is comparatively low, about 3.5 times as long as high. Both laminae enclosing an angle about 90^{o}. Ventral lamina of AVL about one and a half times as long as broad. PVL plate with a well-pronounced high dorsal corner; lateral lamina from about two and a half to three times as long as high; ventral lamina from 1.8 to 2.2 times as long as broad. MV plate is relatively large. Pectoral fin fairly robust, moderately long and narrow. Proximal segment is about 4.5 times as longs as broad in large individuals; distal segment is narrow, rounded in transverse section. Cd_5, Cv_5 and Mm_5 are present. Lateral and median spines of proximal segment are comparatively short and gently defined. Cd_1 plate about 2.9 times as long as broad. Cv_1 plate from about 2.8 to 3.3 times as long as broad. Ml_2 plate about 5.2 times as long as broad. Ornamentation typically reticulate, in small individuals of a fairly regular fine-meshed network of anastomosing ridges without distinct tubercles. Ornament in quite lagre individuals retaining an on the whole reticular character, with often concentrically arranged ridges. It is often 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 are also often with tubercular ornamentation. The ornament become smooth on the pectoral fin; it is well defined only in the anterior part of the Cd_1, Cv_1 and Ml_2 plates. Distal segment bears the gently defined striated ornament.

M a t e r i a l. LDM 43/675, 99/1, 84/67, 3 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.

L o c a l i t i e s. The type locality of *Bothriolepis maxima* is the outcrop of the Ogre Formation sandstones at the Imula River not far from Lankserde hamlet. Other material came from other outcrops at Imula River near Kalnarāji hamlet and Vītiņi hamlet, exposure and caves Velna Ala at Abava River, outcrop at Mūsa River close to Ceraukste village, 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. Outcrop of sandstones, clays and sands of the Nadsnezha Beds at Lovat' River close to Kurskoye Gorodišche village and at the middle current of Lovat' River near Luka village; exposures along the banks of Lower Paluitsa and Upper Paluitsa Rivers surrounding Shugozero village, Russia.

H o r i z o n. The Katleši Formation of the Snezha Regional Substage, Middle Frasnian. The Ogre Formation of the Pamūšis Regional Substage and Prilovat' Beds.

R e m a r k s. *Bothriolepis maxima* is well described by W.Gross (in Stensiö, 1948) and its description is not repeated here.

Bothriolepis evaldi Lyarskaja, 1986

Plate 7; Text-fig. 8

Bothriolepis evaldi: Lyarskaya, 1986, p.123-130; text-figs.1-3; pl.I,II.

H o l o t y p e. Articulated head-shield, trunk-armour and pectoral appendages LDM 67/86.

D i a g n o s i s. Small *Bothriolepis* with a median dorsal armour length reaching about 50 mm. Breadth/length index of trunk armour about 95. Breadth/length index of the head-shield 140-157. Rostral margin of the head-shield is strongly convex. Orbital fenestra is relatively small, broad, slightly less than twice as broad as it is long. Praemedian plate is short and broad. Nuchal plate is arched, moderately broad, length/breadth index of 69.

Trunk-armour is 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 are well marked. Median dorsal ridge well defined posteriorly the tergal angle. Ventral wall of the trunk-armour is relatively narrow, breadth/length index 43-48. AMD is broad, breadth/length index 84-108. It is arched, with right and left laminae forming an angle of about 128°. Anterior margin is 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 is moderately broad with pronounced posterior corner. Dorsal lamina of MxL is 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 is 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.

M a t e r i a l. 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.

L o c a l i t i e s. The type locality Kalnamuiža-1 is cliff at the left bank of Amula River down water-mill Kalnamuiža with grey sandstones and thin layers of blue marls. Other material comes from an outcrop exposing similar deposits at the right bank of Kaibala River 200 m from estuary.

H o r i z o n. All material came from the Middle Frasnian, the Rembate Member of the Ogre Formation (Lyarskaya, 1986).

D e s c r i p t i o n. 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: pl. 7, fig. J) 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 (pl. 7, fig. D) 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, breadth/length index is 140-157, 145 on the average, but reaches only 120 in medium-sized individual. The head-shield is strongly vaulted both rostrocaudally and transversely. The rostral margin is convex, shorter than the posterior margin. The antero-lateral corners (alc) and a shallow prelateral notch (nprl) is clearly defined only in individuals of medium size. The obtected nuchal area (nm) is short, broadest on the Nu plate. The orbital fenestra is relatively not large, but very broad with a breadth/length index about 168-196, 185 on the average. Preorbital recess (prh) is probably of simple type (Young, 1988).

The visceral skull surface shows the normal features. The very broad otico-occipital depression (ood) is well defined by the paramarginal cristae (cr.pm). The median occipital crista (cr.o) is well developed. The transverse nuchal crista is prominent. The median ridge (mr) sharing the broad paired pits (g) of Pp plate is low.

The praemedian plate is broad, much broader than it is long in small specimens with breadth/length index 150-182, which decreases to 103 in largest individuals. It is broadest at the infraorbital sensory groove or rostral margin. The rostral margin is convex, it is 1.2-1.4 times longer then the almost straight orbital margin. There is median elevation inside the rostral margin. The nasal notch (pnn) on the orbital margin can be recognized only slightly in medium-sized specimen LDM 280/1. The infraorbital sensory groove crosses the plate in its anterior part.

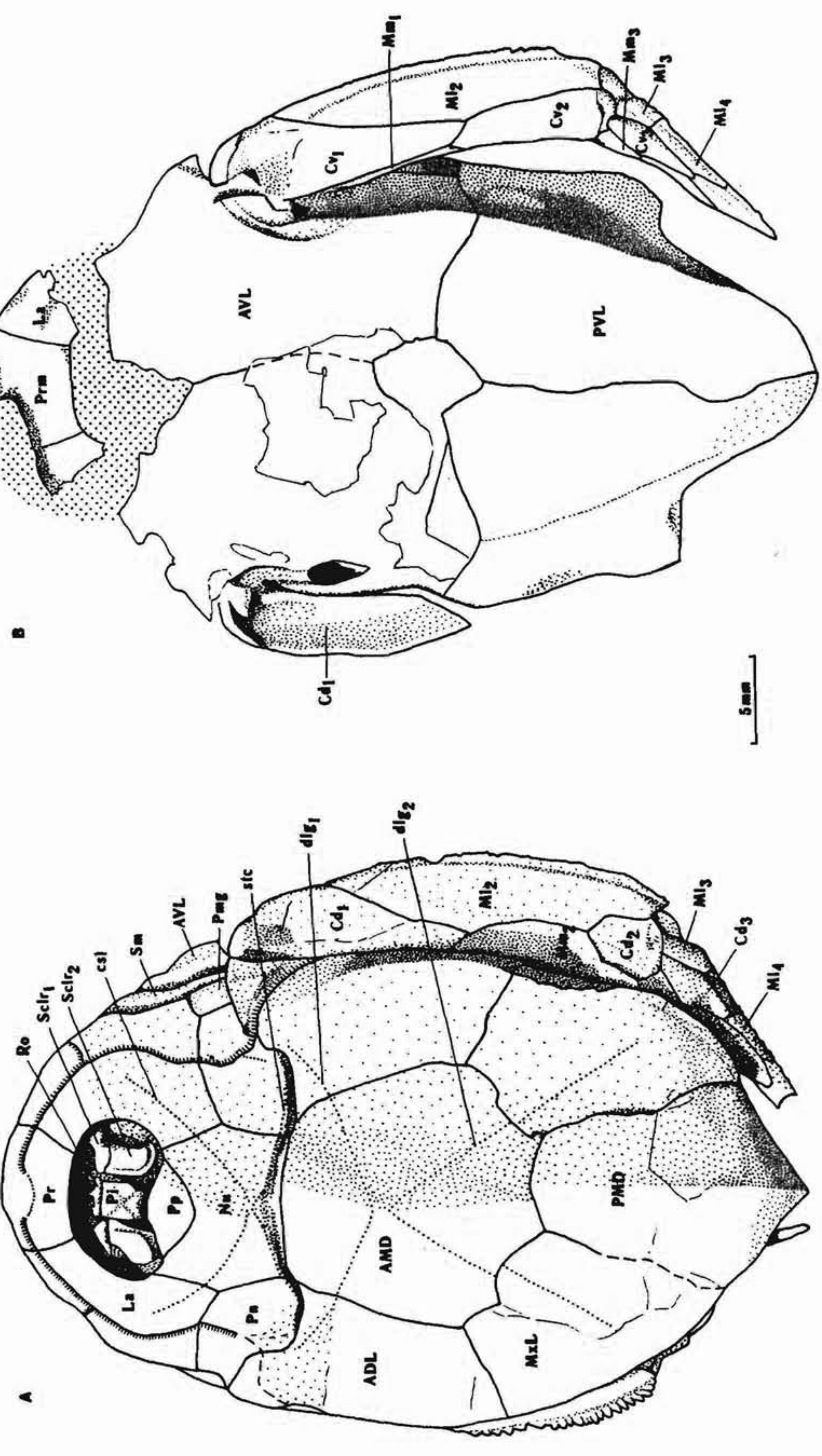
The lateral plate is moderately broad with length/breadth index 126-143, 134 on the average. The infraorbital sensory groove crosses the plate in its anterior part not far from the orbital and lateral margins. The central sensory line groove (csl) usually is finished at the level of the middle of orbital fenestra length, sometimes it extends almost to the anterior margin of the orbital fenestra. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined.

The pineal plate (text-fig. 8 A) is moderately narrow, slightly longer than it is broad. The all four margins are concave. There is a broad unornamented area (sp) along the posterior margin. Position of the pineal pit is marked on the outer surface by the pineal elevation.

The postpineal plate is broad in small individuals and of moderate width in maturity, length/breadth index varies from 44 to 55. As in other species the anterior margin is strongly convex in small specimens and became more straight with increasing size.

The nuchal plate is arched, moderately broad with a length/breadth index 64-76, 69 on the average. The plate is broadest across the lateral corners. 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 (mppr) is weakly defined. The central sensory line groove is clearly distinct. 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 plates. The external openings for the endolymphatic ducts ($d.end_2$) are rather large, closely set one to another. Postorbital crista (cr.pto) on the visceral surface is low, clearly seen only in largest individuals. Specimen LDM 67/39 shows very unusual feature: Nu plate is fused with the Pp plate.

Text-fig.8. A, B, *Bothriolepis evaldi* Lyarskaja. 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 Cd_1 plate LDM 67/3 in ventral view, with dotted space showing the matrix. Kalnamuiža, left bank of Amula River, Latvia. Ogre Formation. x3.


A
Ro
$Sclr_1$
$Sclr_2$
csl
Sm
AVL
Pmg
stc
dlg_1
dlg_2
Cd_1
Ml_2
Cd_2
Ml_3
Cd_3
Ml_4
Pr
Pi
Pp
Nu
La
Pn
AMD
ADL
MxL
PMD
B
La
Prm
AVL
PVL
Cv_1
Mm_1
Ml_2
Cv_2
Mm_3
Ml_3
Ml_4
Cd_1
5mm

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

The postmarginal plate is broad with lateral margins longer than the median margins.

The sclerotic ring is preserved in some specimens. Its features seems to be similar to that of the ring of *B.hydrophila* (Ag.) (Miles, 1968).

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

The trunk armour is broad, breadth/length index 87-99, 95 on the average. 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 ventral wall is long and relatively narrow, its shape and proportions are similar to that of *B.prima*; breadth/length index 43-48. The dorso-lateral and ventro-lateral ridges are well marked.

The anterior median dorsal plate is broad, broader then it is long in medium-sized individuals, breadth/length index about 84-108, 98 on the average. The AMD plate is arched, with right and left laminae forming an angle at the level of lateral corners of about 128^{o}. The anterior margin may be weakly concave or convex, but most often it is fairly straight. It is moderately broad and 1.1-1.6 times as long as the posterior margin (1.3 on the average). 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. 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. 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*: AMD overlaps the MxL by the anterior part of the posterior division of the lateral margin. The anterior oblique dorsal sensory line grooves (dlg_1) are well defined on the plates of small individuals. The posterior oblique dorsal sensory line grooves (dlg_2) are also well defined.

The visceral surface of the AMD shows a moderately broad levator fossa (f.retr), which is limited by the well defined postlevator cristae (cr.pl). The anterior ventral pit (pt_1) and the median ventral ridge (mvr) are weakly defined. The median ventral groove (grm) is gently defined only in individuals of medium size.

The posterior median dorsal plate is arched, moderately broad, breadth/length index 88-105, 95 on the average. The posterior margin is strongly convex, it bears pronounced posterior corner. The width of the anterior margin comprises 44-55% of total breadth (50%

on the average). The lateral and postero-lateral corners are well defined. The median dorsal ridge is strongly developed. The median ventral groove is slightly defined on the visceral surface of the plate. The shallow posterior ventral pit (pt_2) is positioned immediately in front of the strongly developed transverse posterior crista (cr.tp). The ventral tuberosity around the ventral pit is distinct. The postmarginal area (pma) is rather broad.

The anterior dorsal lateral plate is slightly longer than the mixilateral plate in articulated armour. The dorsal lamina is moderately broad, it's breadth exceeds height of the lateral lamina. The dorso-lateral ridge (dlr) is well defined. The postnuchal ornamented corner (pnoa) is sharp, long and narrow.

The dorsal lamina of the mixilateral plate is moderately broad, 1.4-1.6 times 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^{0}. The lateral lamina is moderately high, 2.4-3.2 times as long as it is broad. The dorso-lateral ridge is well defined. The overlap area for the AMD is restricted to half the length of the antero-dorsal margin as in *Remigolepis* (Stensio, 1931). The posterior oblique sensory line groove (dlg_2) in some cases terminates in some distance from the lateral margin, but usually the dorso-ventral pit-line groove crossing the dorso-lateral ridge is present.

The anterior ventral lateral plate is broad, the ventral lamina is 1.4-1.7 times as long as it is broad. The subcephalic division is relatively long and comprises 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 (pl. 7, fig. F). The lateral lamina is moderately high, about twice as long as it is high. Ventro-lateral ridge is well defined. The axillary foramen (f.ax) is rather large and slightly elongated in shape.

The posterior ventral lateral plate 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 and moderately long, it occupies 20-27% of the total PVL plate 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 times as broad as the lateral lamina high. The ventro-lateral ridge (vlr) is well developed.

The median ventral plate is typically developed, the length/breadth index is 1.1 in LDM 67/54.

The pectoral fin is represented mostly by articulated bones. The proximal segment is about 1.9 times 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 Cd_1 is of moderate size with length/breadth index varying from 2.7 to 3.3, 3 on the average. The Cv_1 is slightly longer than the Cd_1 and have similar proportions. The Ml_2

is 4.2-4.6 (4.4 on the average) as long as it is broad. The distal segment shows Cd_3 and Cd_4, 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 Cd_1 the ornament is radially arranged, on the distal segment it consists of longitudinal gently defined ridges. The T plate has almost smooth surface.

D i s c u s s i o n. Most part of materials on *Bothriolepis evaldi* from the type locality shows the following features, which can be considered as of an immature nature: (1) the proportionally large orbital fenestra; (2) the breadth of the Prm plate; (3) the shape of the Pp plate with strongly convex anterior margin; (4) the relatively broad lateral division of the Pn plate; (5) the poor development of the median ventral ridge on the visceral surface of the AMD plate; (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 known individuals from Kaibala locality remain the strongly developed dorsal median ridge. These specimens are very important because they demonstrate that *B.evaldi* does not comprise juveniles of the larger, contemporaneous species *B.maxima* Gross, which occurs with *B.evaldi* in the Ogre Formation. *B.evaldi* resembles *B.maxima* Gross by many features: (1) broad Nu plate; (2) shape and proportions of the AMD and ADL plates; (3) shape of the postnuchal ornamented corner of the ADL; (4) position of the tergal angle etc. Nevertheless *B.evaldi* differs from *B.maxima* in its (1) much smaller size; (2) much broader anterior margin of the AMD plate; (3) position of the tergal angle; (4) shape and proportions of the PMD and PVL plates; (5) strongly developed dorsal median, dorso-lateral and ventro-lateral ridges. Resemblances and differences between this two species as they described by Lyarskaya (1986) could be explained mostly by allometric pattern of growth of *B.evaldi*.

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

B.evaldi resembles *B.prima* from the Main Devonian Field and *B.hydrophila* (Ag.) (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 plate. *B.evaldi* differs from *B.hydrophila* in its (1) smaller size; (2) much broader dorsal wall of the trunk armour; (3) shape and proportions of the AMD plate; (4) shape of the postnuchal ornamented corner of the ADL plate; (5) narrower ventral wall of the trunk armour; (6) shorter proximal segment of the pectoral fin.

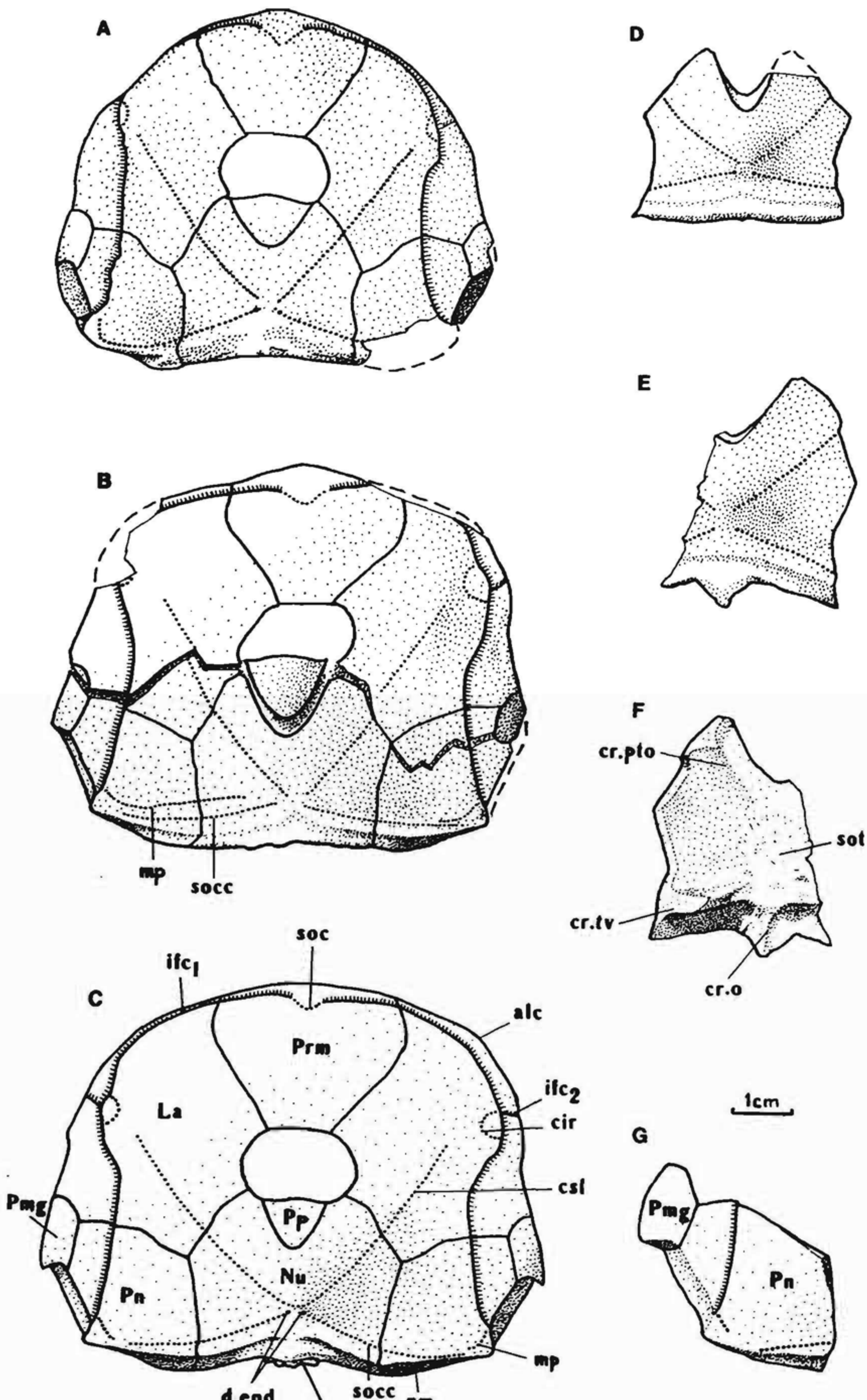
Bothriolepis curonica Gross, 1942

Plates 8-11; Text-figs. 9, 10

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

D i a g n o s i s. Rather large *Bothriolepis* with a median dorsal armour length of at least 240 mm. Dorsal wall of moderate width. Breadth/length index of the trunk-armour about 77. Breadth/length index of the head shield of 130. Anterior margin of the skull roof is rounded. Orbital fenestra is relatively small, long and narrow. Praemedian plate broad, the orbital margin is much shorter than the rostral margin. Nuchal plate is moderately broad, length/breadth index of 84, with very short orbital facetes. Supraoccipital groove and middle pit-line are presented. AMD is relatively narrow, breadth/length index 83. Anterior margin of the AMD is relatively short. PMD is broad with narrow anterior margin. Median dorsal ridge poorly developed in the posterior part of the 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 long as it is broad. Ornamentation is fine and basically of reticular type, in quite large individuals becoming smoothed.
H o l o t y p e. Head-shield LDM 15/32 (pl.8, fig. A).
M a t e r i a l. LDM 15/33 (AMD, PMD), 15/34, 15/121, 65/110-118, 65/121, 65/123, 65/130, 65/133, 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.
L o c a l i t i e s. The type locality is an outcrop exposing sandstones of the Amula Formation and lower part of the Eleja Formation on the right bank of Imula River not far from Bienes hamlet (collection LDM 15). Other material (collections LDM 65, 89, 98) comes from the outcrop containing the stratotype of the Amula Formation and dolomite marls, clays and siltstones of the Eleja Formation at the right bank of Amula River 1 km up from the water-mill Kalnamuiža.
H o r i z o n. All material came from the probably lowermost Upper Famennian, the Eleja Formation (Lukševičs, 1987).

Text-fig. 9. *Bothriolepis curonica* Gross. A-C, head-shields in dorsal view. A, LDM 98/12. B, LDM 98/86. C, attempted reconstruction, based on LDM 89/1. D-F, Nu plates. D, LDM 98/13 in dorsal view. E,F, LDM 98/20 in dorsal and visceral views. G, Pn and Pm plates LDM 98/18 in dorsal view. Kalnamuiža, right bank of Amula River, Latvia. Eleja Formation.


A
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Pmg
Pp
Pn
Nu
d.end
mppr
socc
nm
mp
cr.pto
sot
cr.tv
cr.o
1cm
Pmg
Pn

D e s c r i p t i o n. This species is well represented in clays 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 fin. Most are from individuals of moderate size. The plates are usually flattened, often deformed. The skull roof is moderately broad, breadth/length index is 130 on the average (pl. 8, figs A-D; text-figs. 9 A-C). The rostral margin is convex, rounded, usually slightly longer than the posterior margin. The head-shield is weakly vaulted both rostrocaudally and transversely, but the anterior part of the Prm and La plates is strongly curved. The antero-lateral corner (alc), the prelateral notch and the lateral process are weakly defined. The obtected nuchal area (nm) is short, broadest on the Nu plate, with slightly defined lateral processes; the median process (mppr) is usually well developed. The orbital fenestra is relatively small, long and narrow, with a breadth/length index varying from 175 in individuals of moderate size to 150 in largest individuals. This feature separates *B.curonica* well from all the other *Bothriolepis* representatives from the Main Devonian Field.

The praemedian plate is weakly arched, broad, breadth/length index 123-148. It is broadest at the infraorbital sensory groove or rostral margin. *B.curonica* differs well from the other species in that the convex rostral margin is 3 times longer than the slightly concave orbital margin. The infraorbital sensory groove (ifc_1) crosses the plate close to its rostral margin. The anterior section of the supraorbital sensory line (soc) is well defined.

The lateral plate is short and broad with the length/breadth index 120-128, 124 on the average. The rostral margin is moderately broad, the antero-median corner is sharp and well defined. The infraorbital sensory groove crosses the plate in its anterior part not far from the orbital and lateral margins. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined. The central sensory line groove (csl) is finished at the level of the anterior margin of the orbital fenestra close to the semicircular pit-line groove.

The postpineal plate is narrow and long, length/breadth index varies from 69 to 83, 76 on the average. The anterior margin is convex with two slightly defined lateral notches.

The nuchal plate (text-figs. 9 D-F) is moderately broad with a length/breadth index about 84. The plate is broadest across the lateral corners. The anterior division of the lateral margin is a little shorter than the posterior division. The shape of the posterior margin is variable, it bears the posterior process (mppr). The orbital facets are very short. The supraoccipital grooves (socc) are long and extend laterally to the Pn plates. The external openings for the endolymphatic ducts ($d.end_2$) are closely set one to another. The postorbital crista (cr.pto) and the transverse nuchal crista (cr.tv) on the visceral surface are prominent.

The paranuchal plate is of moderate breadth, the length/breadth index about 86. The lateral division of the Pn is relatively narrower than in Frasnian *Bothriolepis* and is composing 34-45% (38.7 on the average) of the general breadth of a plate. The supraoccipital groove (socc) terminates usually at the level of the middle of the plate posterior margin. The middle pit-line groove (mp) is always presented, sometimes it is very long (LDM 98/86: pl. 8, fig. D; text-fig. 9 B) or (in LDM 98/3,7,12, 89/5: text-fig. 9 A) it fuses with the supraoccipital groove.

The postmarginal plate is usually elongated, 1.2-1.9 times as long as it is broad, with the lateral margins longer than the median margins.

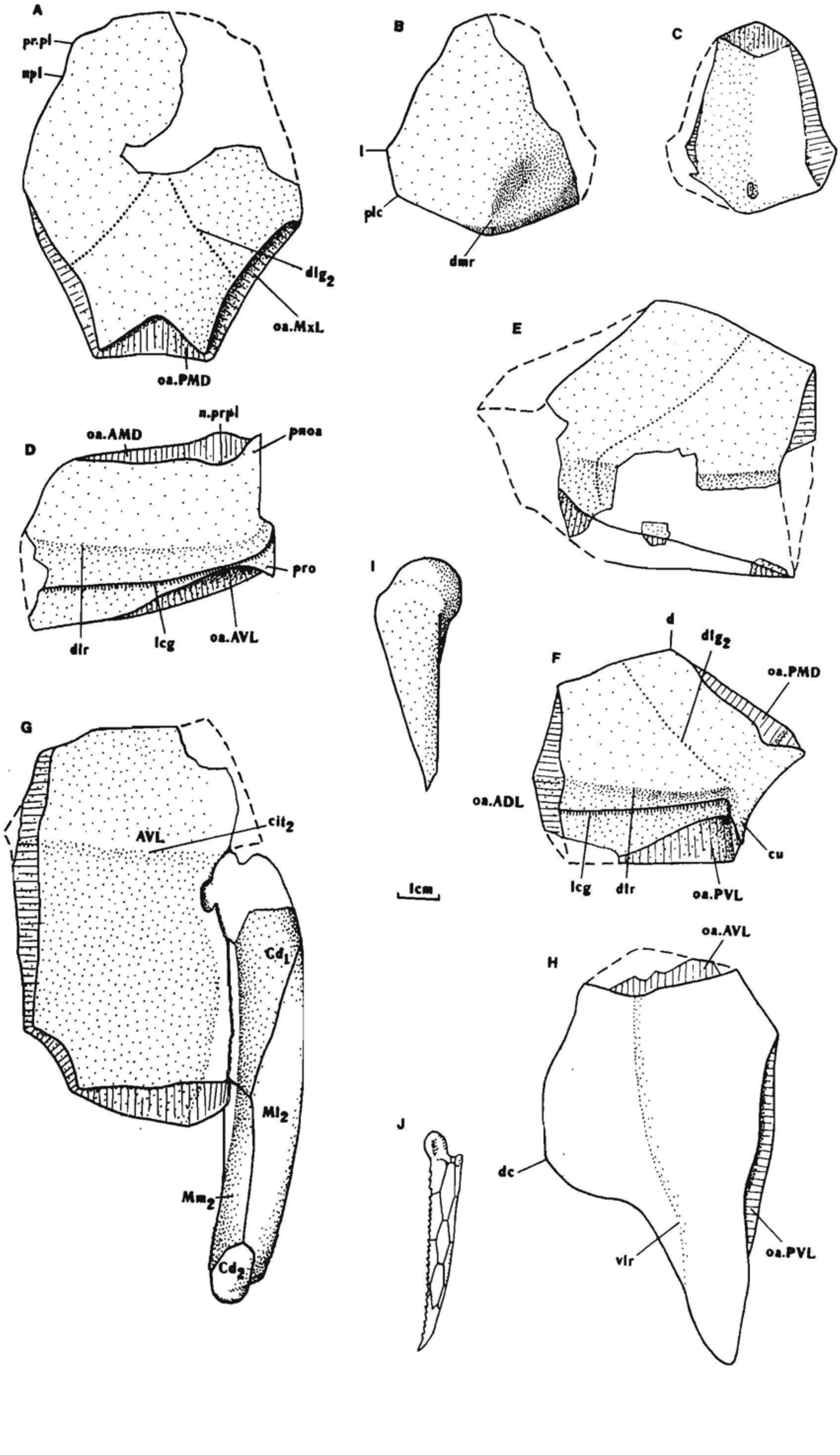
The trunk armour is relatively narrow, with breadth/length index 77 in individuals of the moderate size. It is relatively low, with a lateral wall more than 3 times as long as high; in comparison with some other species it is rather flattened with low dorsal wall. The length of the dorsal wall, probably, is more than 240 mm. The median dorsal ridge is weakly defined only in the posterior part of the PMD. The dorso-lateral and ventro-lateral ridges are well marked. It is impossible to measure the angles between trunk shield walls due to deformations of the plates. The ventral wall of the trunk shield is narrow, with the breadth/length index about 53. The subcephalic division is relatively long and broad, the subanal division is long and narrow.

The anterior median dorsal plate (pl. 9, figs. A, B; text-fig. 10 A) is weakly arched, relatively narrow, breadth/length index about 83. The anterior margin is weakly convex, relatively narrow and slightly longer than the posterior margin. The antero-lateral and lateral corners, as well as the postlevator processes (pr.pl) are well defined. The posterior division of the lateral margin is 1.4-1.6 times shorter than the anterior division. The tergal angle (dma) is situated slightly anteriorly the middle of the plate. There is no median dorsal ridge. Overlap areas for ADL and MxL are normally developed as usually in *Bothriolepis*.

The posterior median dorsal plate (text-figs. 10 B, C) is broad in comparison with the AMD, breadth/length index about 95. 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 has no pronounced posterior corner. The lateral (l) and postero-lateral (plc) corners are well defined. The median dorsal ridge (dmr) is present only in the posterior third of the plate.

The dorsal lamina of the anterior dorsal lateral plate (pl. 9, fig. C; pl. 10, figs. A, B; text-fig. 10 D) is of moderate breadth, 3 times as long as it is broad. It bears large postnuchal ornamented corner (pnoa).

Text-fig.10. *Bothriolepis curonica* Gross. A, AMD LDM 98/21 in dorsal view. B, PMD LDM 98/36 in dorsal view. C, PMD LDM 98/35 in visceral view. D, ADL LDM 98/58. E, MxL LDM 98/53. F, MxL LDM 89/2. G, AVL in visceral view with articulated proximal segment of the pectoral fin in dorsal view LDM 98/78. H, PVL LDM 98/45 in ventral view. I, Cv_1 LDM 98/90. J, distal segment of the pectoral fin LDM 89/4. Kalnamuiža, right bank of Amula River, Latvia. Eleja Formation.


A
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oa.MxL
oa.PMD
B
l
plc
dmr
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D
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n.prpl
pnoa
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oa.AVL
I
d
dlg2
F
oa.PMD
oa.ADL
cu
lcg
dlr
oa.PVL
G
cit2
AVL
Cd1
Ml2
Mm2
Cd2
1cm
oa.AVL
H
J
dc
vlr
oa.PVL

The mixilateral plate (pl. 10, figs. C, D; text-figs. 10 E, F) is moderately long. The dorsal lamina of the plate is narrow, slightly less than twice as long as it is broad. The dorsal corner is clearly seen. The lateral lamina is low, more than 3 times as long as it is broad. The posterior oblique sensory line groove (dlg_2) usually terminates in some distance from the lateral margin; LDM 98/53 (text-fig.16E) shows dlg_2 crossing the dorso-lateral ridge. In LDM 98/54, which belonged to the small individual, the dlg_2 is connected with the main lateral line groove (lcg). The dorso-lateral ridge (dlr) is well defined both in the ADL and MxL plates.

The anterior ventral lateral plate (pl. 10, figs. E, F; text-fig. 10 G) is relatively narrow, compared with that in Frasnian *Bothriolepis*: the ventral lamina is 1.9-2 times as long as it is broad. The subcephalic division is moderately long and comprises 21-25% (22.5 on the average) of total length of the ventral lamina. The ventral lamina 3.8 times as broad as the lateral lamina high in LDM 98/30. The anterior margin of the ventral lamina is rounded without clearly defined corners. The lateral lamina is low. The right AVL overlaps the left AVL by very narrow overlap area.

The posterior ventral lateral plate (pl. 11, figs. B, C; text-fig. 10 H) has variable proportions. It is relatively narrow, narrower than that in most other *Bothriolepis*: the ventral lamina is 2.4-2.7 times as long as it is broad. The subanal division also is narrow and moderately long, it occupies about one fifth-one third (22-32%) of the total PVL plate length. The lateral lamina is moderately high, 2.3-2.7 times long as it is high. The ventral lamina about 1.3 times as broad as the lateral lamina high. The ventro-lateral ridge (vlr) is clearly defined both in the AVL and PVL plates.

The median ventral plate is unknown, but the shape of the AVL and PVL plates suggests the small size of the slightly elongated MV.

The pectoral fin is represented by some disarticulated bones, and six specimens showing articulated plates of the proximal segment associated with the AVL plate. The proximal segment bears small rarely set lateral and mesial spines, the lateral spines are larger than the mesial ones. It is very characteristic for *B.curonica*, that 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. The Cd_1 is of moderate size with length/breadth index varying from 2.7 to 3.7 (3.3 on the average). The Cv_1 is gently longer than the Cd_1 and slightly more elongate (L/B 3.4). *B.curonica* has unusually elongated Ml_2 plate. The Cd_2 is slightly longer than it is broad. Specimen LDM 89/4 (pl. 10, fig. G; text-fig. 10 J) is an articulated distal segment, which is very long and narrow, length/breadth index 5.7, and contain the Cd_5 plate. The distal segment is not adorned with marginal spines, the lateral spines are sharp and proximally directed.

The ornamentation is fine and basically of reticular type, in quite large individuals becoming smoothed. 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, radially arranged on the anterior part of the Cd_1 and Cv_1; 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.

D i s c u s s i o n. *Bothriolepis curonica* is particularly characterized by the short orbital margin of the Prm, the long and narrow AMD and slender pectoral appendage. These features separate *B.curonica* from all other well-known Baltic and Russian species. Among the other species of *Bothriolepis*, *B.curonica* is morphologically closest to *B.leptocheira* Traquair from Scotland (Miles, 1968). Both species are similar in (1) the shape and proportions of individual plates of the head shield; (2) the shape and proportions of the AMD; (3) the slender pectoral fin. However, *B.curonica* differs from *B.leptocheira* in its (1) larger size; (2) presence of the middle pit-line groove; (3) more elongated AVL; (4) more smooth ornamentation. *B.jarviki* Stensiö (1948) from Greenland resembles *B.curonica* by some features, but differs from it by the other shape and proportions of the Prm, Pp, Nu, PMD and the ornamentation. *B.curonica* closely resembles also *B.jeremejewi* Rohon (1899) 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, PIN and GM 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 morphologically closely related or not.

Bothriolepis ornata Eichwald, 1840

Plates 13-21; Text-figs.11-20

Bothriolepis ornatus: Eichwald, 1840a, p.78.
Bothriolepis prisca: Eichwald, 1840b, p.425.
Bothriolepis ornata: Eichwald, 1860, p.1513; pl.CVI, fig.3. Eichwald, 1861, p.451; pl.XXXV, fig.3.
Asterolepis ornata: Eichwald, 1861, p.448 (pars).
Bothriolepis ornata Eichw.: Woodward, 1891, p.225.
Bothriolepis ornata Eichw.: Gross, 1932, p.23, 24.
Bothriolepis ornata Eichw.: Gross, 1933, p.40; pl.IV, figs.7, 14.
Bothriolepis ornata Eichw.: Stensiö, 1948, p.401; text-fig.215-217.
Bothriolepis ornata Eichw.: Obruchev, 1964; pl.VI, fig.2..
Bothriolepis ornata Eichw.: Lukševičs, 1992; p. 65, text-figs.1-4; pl.1-4.
Bothriolepis cf.*ornata* Eichw. - Gross, 1942, p.403, 422 (pars), non text-fig.11.
For full list of synonims before 1932 see W.Gross (1932).

Type specimen. Woodward (1891) has selected MM 116/107 as the lectotype (Eichwald, 1860, p.1513; pl. CVI, fig. 3). It is an anterior median dorsal plate, collected by Helmersen (text-fig. 14 B).

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. Dorsal wall of the trunk armour of moderate width, breadth/length index about 82. Median dorsal ridge poorly developed. Breadth/length index of the head shield of 127. Praemedian plate of moderate breadth, the orbital margin is 1.5 times shorter than the rostral margin. Nuchal plate is arched, relatively narrow, length/breadth index of 85. Paranuchal plate is narrow. AMD is moderately narrow, breadth/length index is about 79-88. Anterior margin of AMD is concave and short. PMD is narrow, ADL has narrow lateral lamina and large postnuchal ornamented corner. Proximal segment of the pectoral appendage is moderately long, 4 times as longs as it is broad. Ornamentation typically reticulate, in quite large individuals becoming coarser and sparser.

Material. From the type locality: MM 5/198, PVL; BMNH P.4600, Ml_1, P.710, MxL; PIN 835/4, Nu. From the locality at Skujaine River near Klūnas hamlet: LDM 43/730, 100/1-65, 100/145-147, 100/336, 100/346, 100/354-368, 100/396-426, 100/441, 100/523, 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, Cd_2.

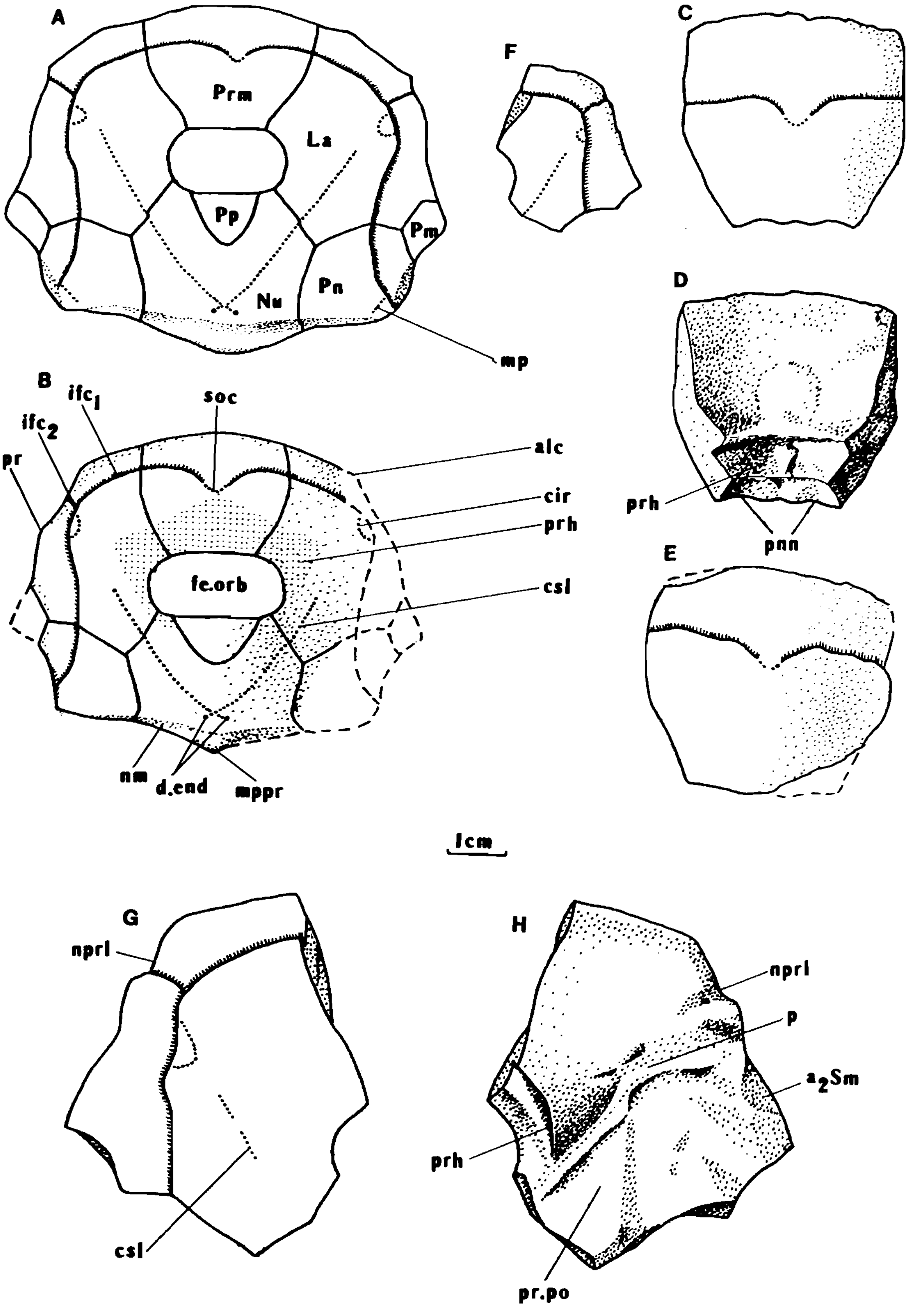
L o c a l i t i e s. The type locality is exposures at Priksha River, Russia. Other material comes from the two outcrops of white and pink sands containing abundant fish bones, dolomite marls and marls at the right bank of Skujaine River down Klūnas village, Latvia. Fragments of plates, undescribed here, which comes from Belaya, Lnyanka and Mshanka Rivers in Novgorod region of Russia, probably would belong to *B.ornata*.

H o r i z o n. Lectotype and the PVL plate MM 5/198 came from the Upper Famennian Lnyanka Beds of eastern part of the Main Devonian Field. All material from Klūnas locality came from the Tērvete Formation of Latvia.

D e s c r i p t i o n. This species 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 the well-grown individuals of moderate size, but there are also some small, as well as quite large specimens. *Bothriolepis ornata* is one of the largest of species of *Bothriolepis*, although it did not quite reach the size of *B.maxima* Gross and *B.gigantea* Traquair. The head shield is of moderate size, breadth/length index is about 127. The skull roof is strongly vaulted both rostrocaudally and transversely. The rostral margin is convex, slightly shorter than the posterior margin, which is weakly convex and bears well defined median process. There are well defined anterolateral corners (alc) and the deep prelateral notch (nprl). The obtected nuchal area (nm) is long, broadest on the Nu plate. The orbital fenestra is relatively short and broad, with a breadth/length 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 is extended to the middle of Prm, lateral horns are not reach the middle of La, as it is in *B.hayi*.

The visceral skull roof surface shows the normal features. The broad otico-occipital depression is well defined by the paramarginal cristae (cr.pm). The antero-lateral corner of the otico-occipital depression (pr.po) is broad in its base and extended nearly to the rostral margin of the orbital fenestra. The postero-lateral corner is rounded and not extends laterally over the middle of the Pn plate's posterior margin, as it is in *B.ciecere*. The transverse lateral groove is moderately broad and clearly defined. A broad shallow depression anteriorly from the antero-lateral corner of the praeorbital recess is the lateral pit (p), which is situated more laterally than mesially. The median occipital crista (cr.o) is relatively low, often it consists of 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 plate is very low.

Text-fig. 11. *Bothriolepis ornata* Eichwald. A, restoration of head-shield based on specimen LDM 100/32. B, head-shield LDM 100/31. C-E, praemedian plates. C,D, LDM 100/34 in dorsal and visceral view. E, LDM 100/396 in dorsal view. F-H, lateral plates. F, LDM 100/44 in dorsal view. G, H, LDM 100/358 in dorsal and visceral view. Skujaine River near Klūnas, Latvia. Tērvete Formation.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The praemedian plate (text-figs. 11 C-E) is moderately broad, breadth/length index about 112. It is broadest slightly posteriorly the infraorbital sensory groove. The rostral margin is convex, 1.7-1.9 times longer than the orbital margin. The orbital margin is straight or weakly concave and bears clearly defined but shallow nasal notch (pnn). The infraorbital sensory groove (ifc_1) crosses the plate anteriorly from its middle part.

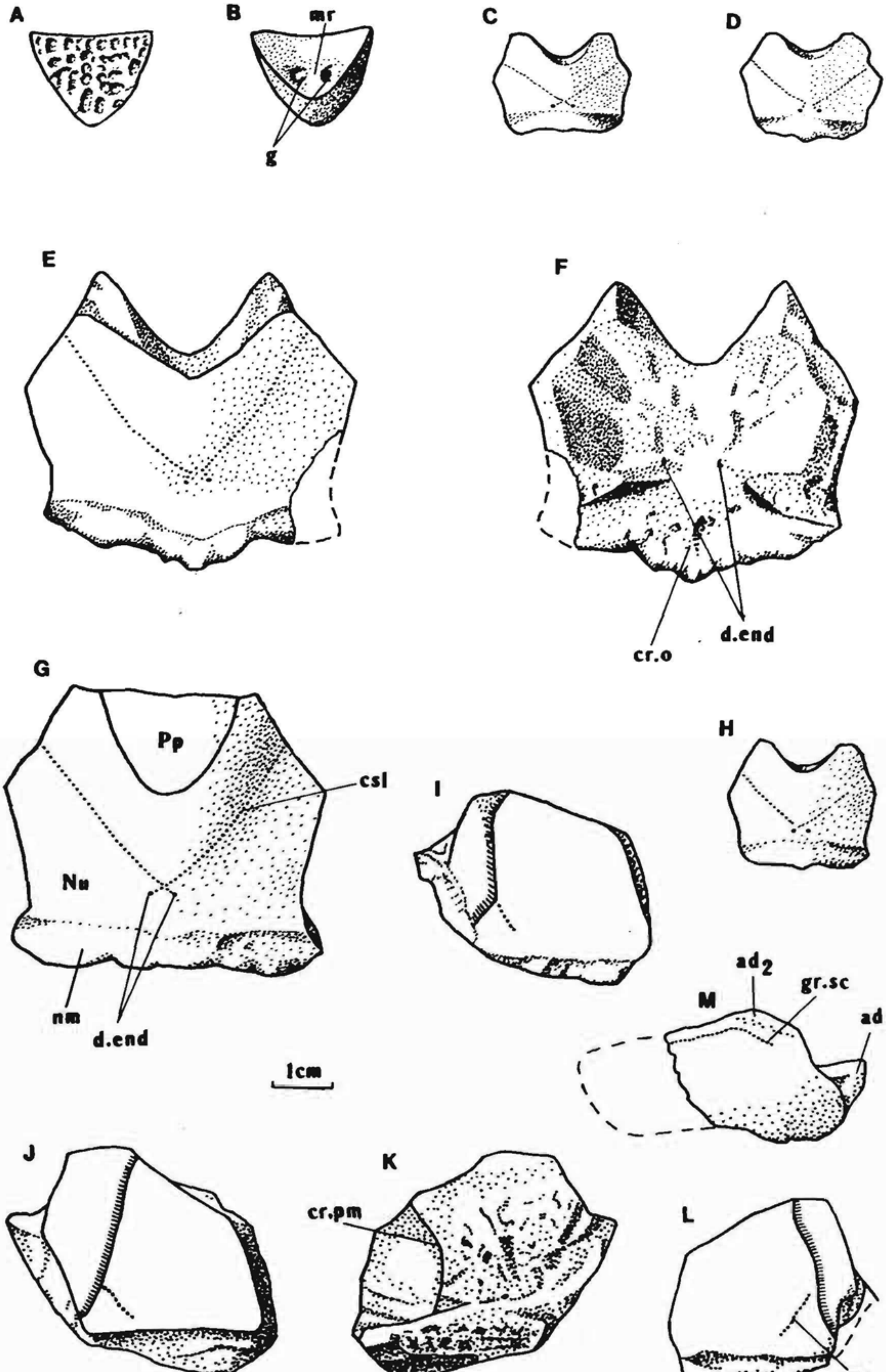
The lateral plate is moderately broad with length/breadth index about 123-139, 132 on the average (pl. 13, figs. D-F; text-figs. 11 G, H). The rostral margin is relatively short and almost straight, the antero-median and antero-lateral corners are well defined. The infraorbital sensory groove (ifc_1) crosses the plate in its anterior part not far from the lateral margin. The central sensory line groove (csl) usually is finished slightly anteriorly the middle of orbital fenestra length, it might be interrupted or very short. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined.

The postpineal plate (text-figs. 12 A, B) is broad, length/breadth 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 nuchal plate (pl. 13, figs. G-L; text-figs. 12 C-H) is vaulted with an angle between right and left halves about 132^{0}. It is relatively narrow, length/breadth index 72-93, 83 on the average. The plate is broadest across the lateral corners. 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 (mppr). The antero-lateral, lateral and postero-lateral corners are well defined. The orbital facets are short. 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 (pl. 13, fig. K; text-fig. 12 E) shows the broad unornamented area along the postpineal notch, which probably was overlapped by the extremely broad Pp plate. As a result the outer surface of this Nu plate is excluded from the contact with the orbital fenestra similar as in *Asterolepis*.

The paranuchal plate (pl. 13, fig. M; text-figs. 12 I-L) is relatively narrow, length/breadth index about 98. The lateral division of the Pn is relatively narrow and composing 50% of the breadth of a median division, which is as long as it is broad. The lateral margin of the plate is short. The plate usually bears a short middle pit-line groove (mp).

Text-fig. 12. *Bothriolepis ornata* Eichwald. A, B, postpineal plate LDM 100/41 in dorsal and visceral view. C-F, H nuchal plates. C, LDM 100/38 in dorsal view. D, LDM 100/39 in dorsal view. E, F, LDM 100/42 in dorsal and visceral view. H, LDM 100/399 in dorsal view. G, nuchal and postpineal plates LDM 100/398 in dorsal view. I, paranuchal plate LDM 100/402 in dorsal view. Skujaine River near Klūnas, Latvia. Tērvete Formation.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ad2
gr.sc
ad1
1cm
J
K
cr.pm
L
mp

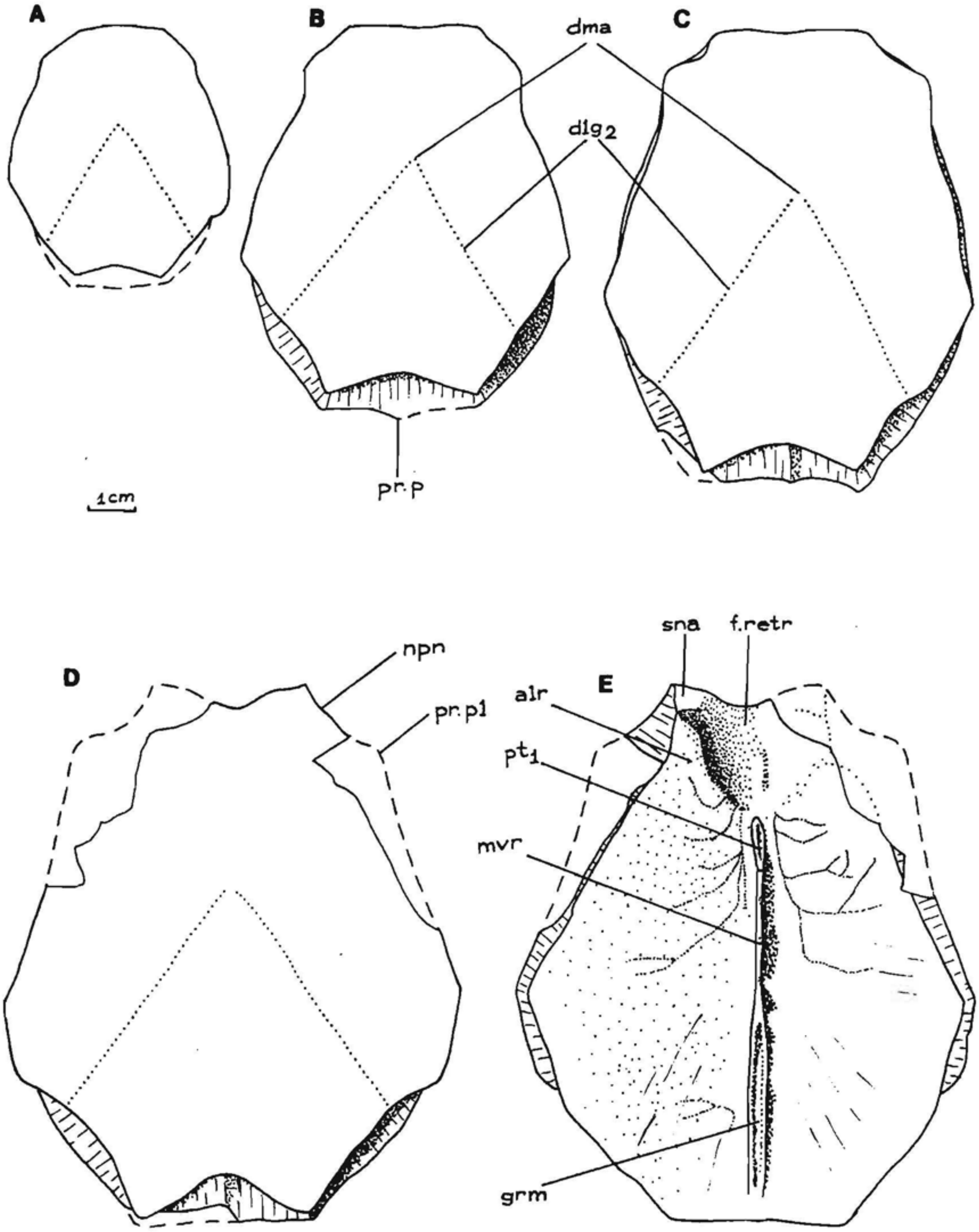
The submarginal (extralateral) plate (text-fig. 12 M) is known from two poorly preserved specimens PIN 1491/92, 1491/93, both are the anterior end of the plate. It is of moderate length. The dorsal margin has a prominent antero-dorsal process. There is a groove (gr.sc) running along the dorsal margin of the ornamented part of the plate, which is similar to that of *B.obrutschewi* (Karatajute-Talimaa, 1966) and *B.macphersoni* Young (1988). It has the character of a sensory groove. A well marked lateral notch is rather deep separating the plate into a short thick anterior division (ad_1) and more thin posterior division (ad_2).

Plasticine reconstruction with large disarticulated plates was used to describe the features of the trunk armour. The trunk armour is relatively low and broad, breadth/length index 82. Length of the dorsal wall, probably, is more than 240 mm in largest individuals and only 50 mm in smallest ones. The dorsal wall is of moderate height, right and left laminae encloses the angle about 132^0. As 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 depression anteriorly the tergal angle is weakly developed as in *B.groenlandica* Heintz (Stensio, 1948).

The anterior median dorsal plate (pl. 14-16; text-figs. 13, 14) is moderately broad, breadth/length index about 79-88, 83 on the average. The always concave anterior margin is narrow, usually shorter than the posterior margin, and 2.2-3.1 times narrower as a total breadth of the plate. The antero-lateral and lateral corners are rounded, the postnuchal notch (npn) is deep and postlevator process (pr.pl) are sharply defined. The posterior division of the lateral margin is 1.4-1.6 times shorter than the anterior division. The tergal angle (dma) is situated in some distance posteriorly the anterior third of the plate. There is no median dorsal ridge. The 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 shape: the outer surface of ADL slightly overlaps AMD. The anterior oblique dorsal sensory line groove (dlg_1) is not present, the posterior oblique dorsal sensory line groove (dlg_2) 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 shows dlg_2 on the left side terminated in front of the postero-lateral margin.

The visceral surface of the AMD (text-fig. 13 E) shows a narrow long 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 (pt_1) 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).

Text-fig.13. *Bothriolepis ornata* Eichwald. AMD plates. A, LDM 100/405 in dorsal view. B, LGI 5/2046 in dorsal view. C, LDM 100/2 in dorsal view. D, E, LDM 100/3 in dorsal and visceral view. Skujaine River near Klūnas, Latvia. Tērvete Formation. x 0.7.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1cm
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f.retr
alr
pt1
mvr
grm

The posterior median dorsal plate (pl. 17; pl. 18, figs. A-D; text-fig. 15) is narrow, breadth/length index about 75-89, 82 on the average. The anterior and posterior margins 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. The PMD plate 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 (pt_2) and strongly developed ventral tuberosity (tb) in large individuals. The crista transversalis interna posterior (cr.tp) is low and smoothed, the postmarginal area (pma) is narrow.

The dorsal lamina (dlm) of the anterior dorsal lateral plate (pl. 19, figs. A-C; text-fig. 16) is relatively long, but due to significant breadth of the postnuchal ornamented corner (pnoa) it is only 2.2 as long as it is broad. The lateral lamina is 3 times as long as it is high. The postnuchal ornamented corner (pnoa) is broad and strongly pronounced. The processus obstans is normally developed. The ADL plate is not simply overlapped by AVL plate, but also at the same time overlaps that plate posteriorly the processus obstans, as in *B.canadensis, B.groenlandica* and *B.maxima*.

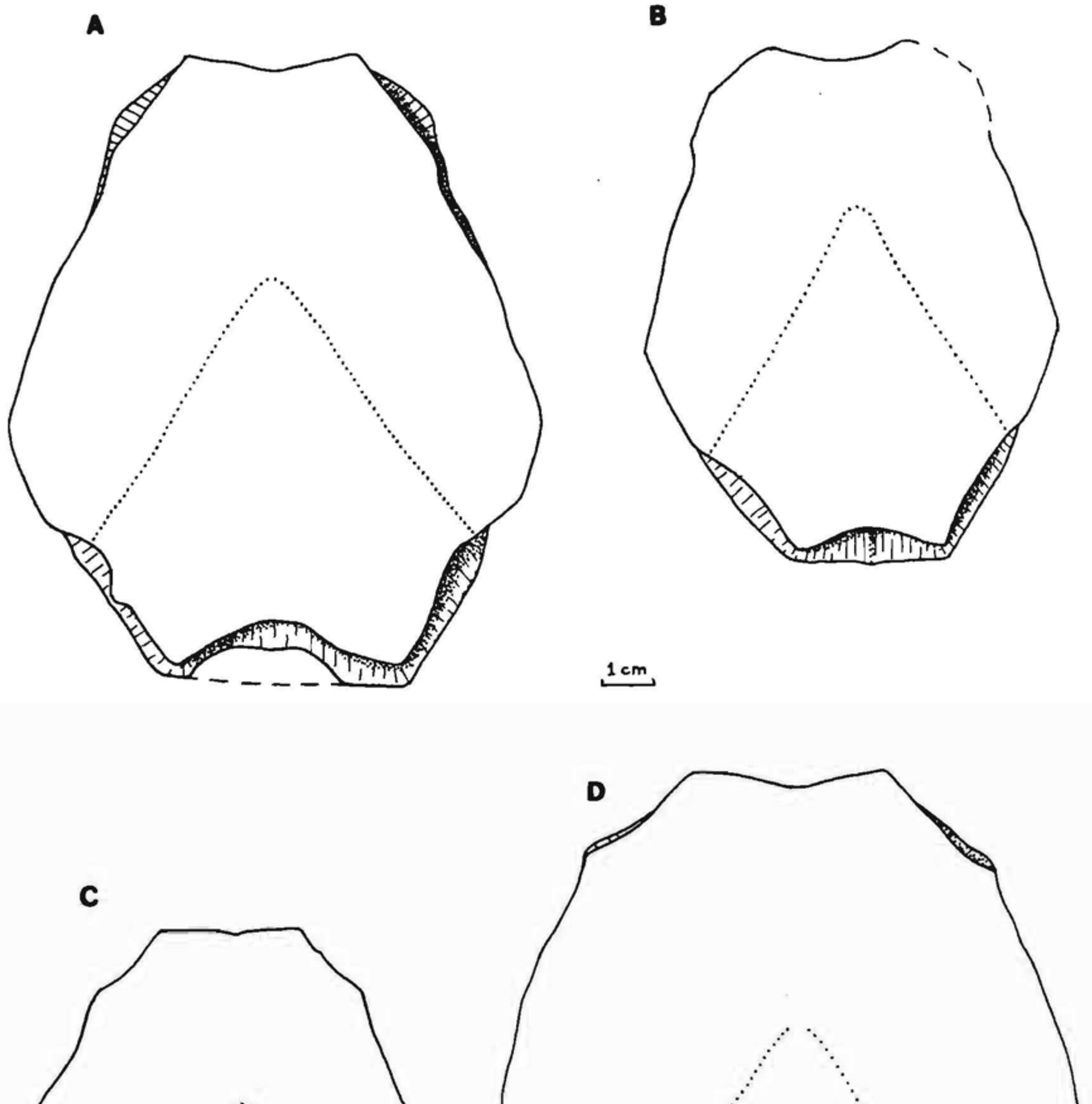
The mixilateral plate (pl. 18, figs. E-G; text-fig. 17) is moderately broad. The dorsal lamina of the plate is less than twice (1.7-1.8 times) as long as it is broad. The lateral lamina is moderately high, 2.5-2.6 times as long as it is broad. The dorsal corner (d) is well defined. The postero-ventral ornamented corner (cu) is long and sharp. The posterior oblique sensory line groove (dlg_2) terminates in some distance from the lateral margin.

Text-fig.14. *Bothriolepis ornata* Eichwald. AMD plates in dorsal view. A, LDM 100/4. B, holotype MM 116/107. C, LGI 5/2078. D, LGI 5/2051. A, C, D, Skujaine River near Klūnas, Latvia. Tērvete Formation. B, Prikscha River, Novgorod region, Lyubitino district, Russia. x 0.7.

Text-fig.15. *Bothriolepis ornata* Eichwald. PMD plates. A,B, LDM 100/408 in dorsal and visceral view. C, LDM 100/354 in visceral view. D, LDM 100/355 in dorsal view. Skujaine River near Klūnas, Latvia. Tērvete Formation.

Text-fig.16. *Bothriolepis ornata* Eichwald. ADL plates. A, LDM 100/364 in dorsal view. B, PIN 1491/89 in dorsal view. C, LDM 100/16 in dorsal view. D, LDM 100/411 in anterior view. Skujaine River near Klūnas, Latvia. Tērvete Formation.

Text-fig.17. *Bothriolepis ornata* Eichwald. MxL plates. A, LGI 5/2058. B, LDM 100/21. C, LDM 100/20. Skujaine River near Klūnas, Latvia. Tērvete Formation.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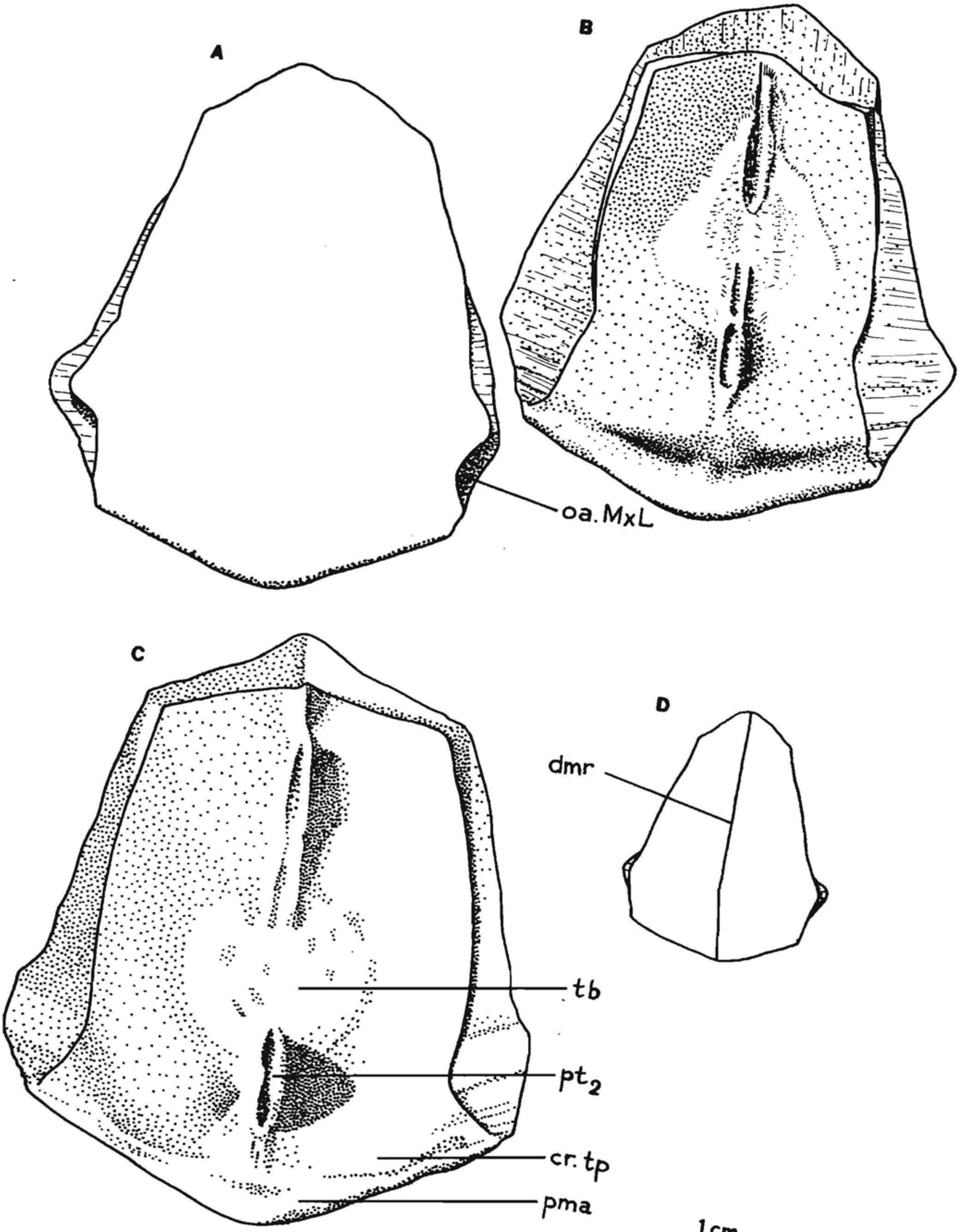
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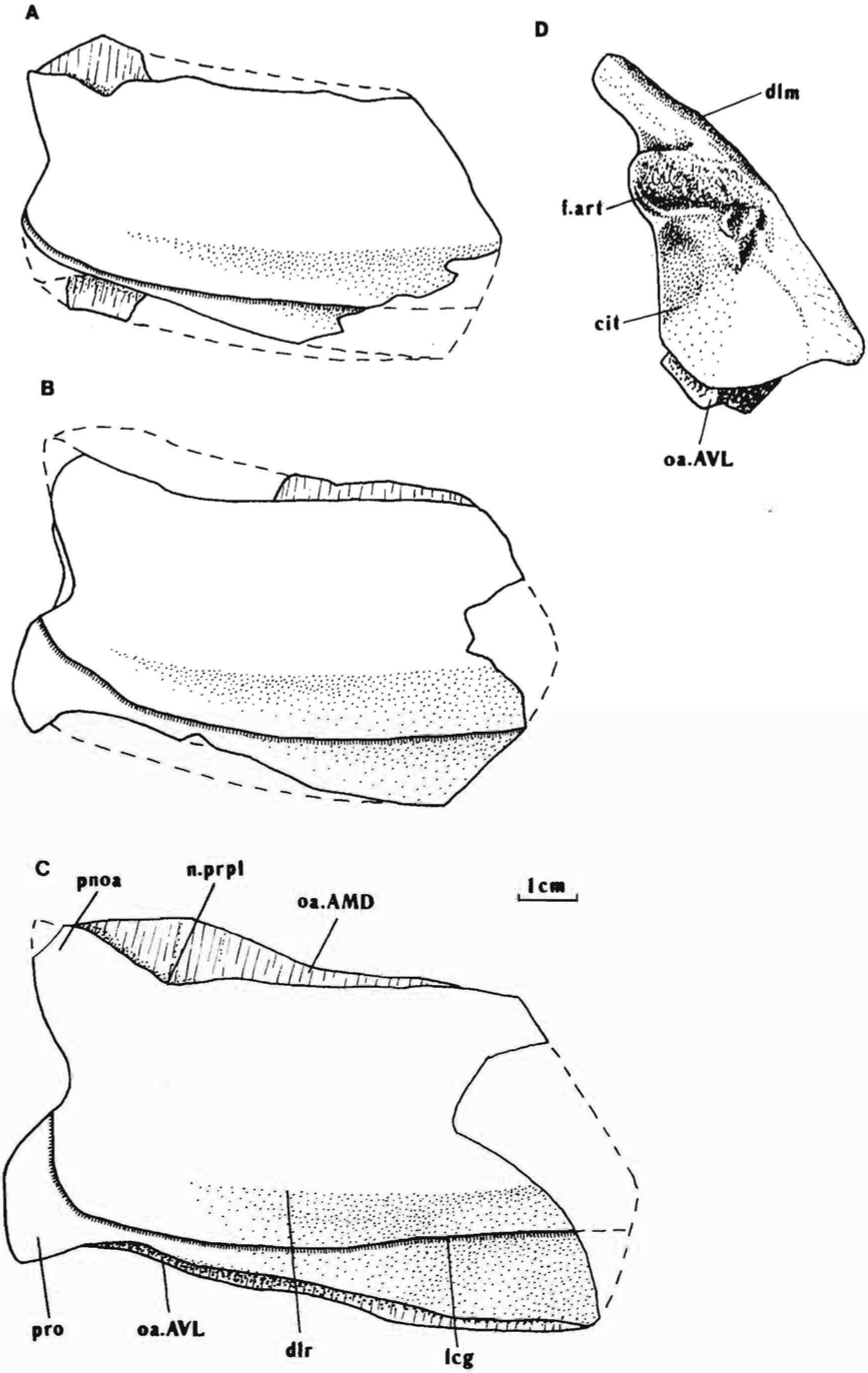
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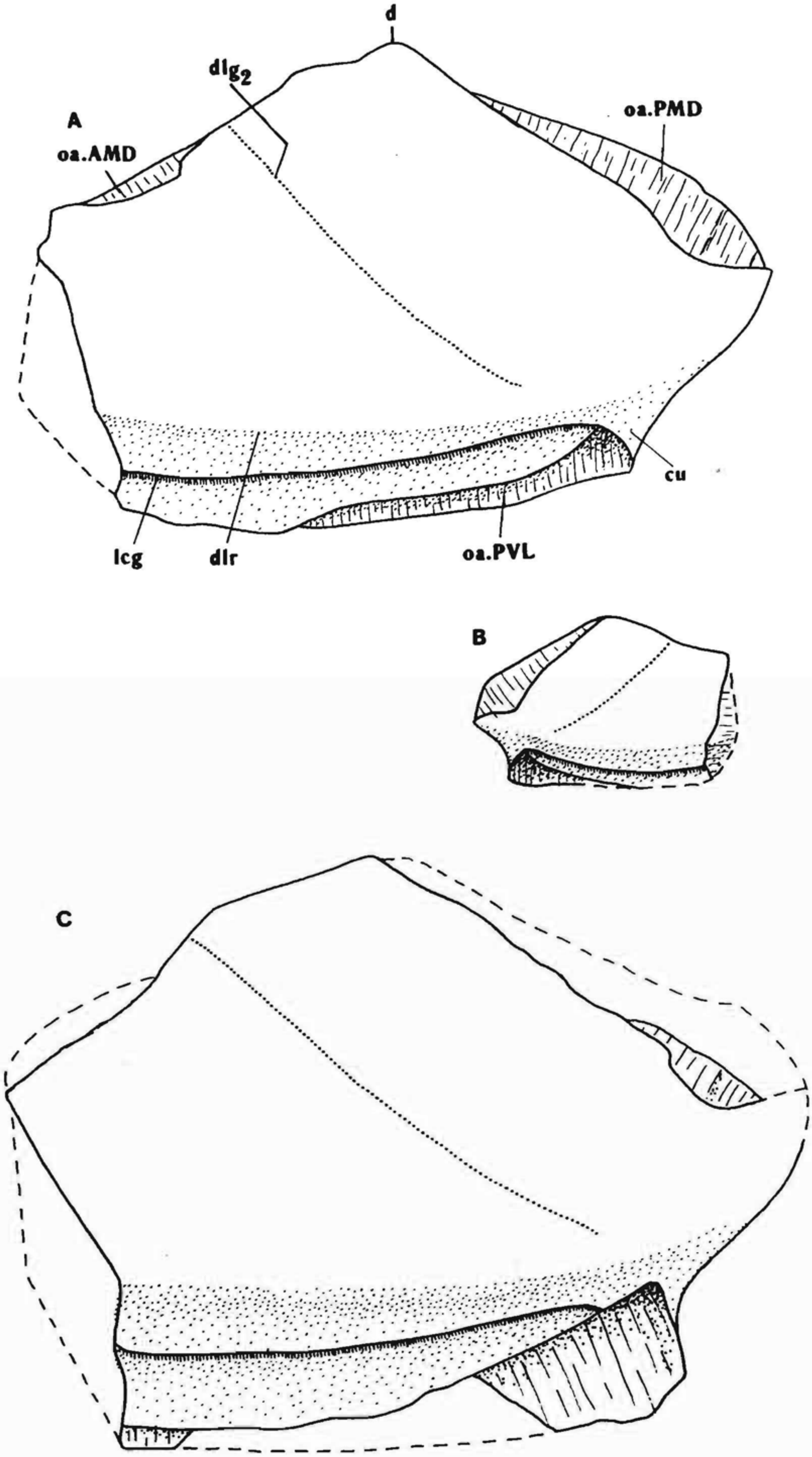
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oa.PVL
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The anterior ventral lateral plate (pl. 19, figs. F, G; pl. 20, figs. A-C; text-fig. 18) is of moderate breadth, the ventral lamina of the single well preserved plate is 1.5 times as long 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. The processus brachialis shows some features previously unknown in other *Bothriolepis* from the Main Devonian Field. 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 shows the funnel pit divided into two divisions by very thin longitudinal wall. Probably this structure is the result of the joint disease.

The visceral surface of the AVL shows the high transverse anterior crista (cit_1) running antero-mesially and the low and broad transverse thickening (cit_2) directed more mesially.

The posterior ventral lateral plate (pl. 19, figs. D-E) has similar proportions to the AVL, as in most *Bothriolepis* species. It is of moderate breadth, the ventral lamina is 2 times as long as it is broad. The subanal division is relatively narrow and moderately long, it occupies about 30% of the total PVL plate length. The lateral lamina is high, about twice as long as it is high. Similar to AVL the left PVL overlaps the opposite PVL.

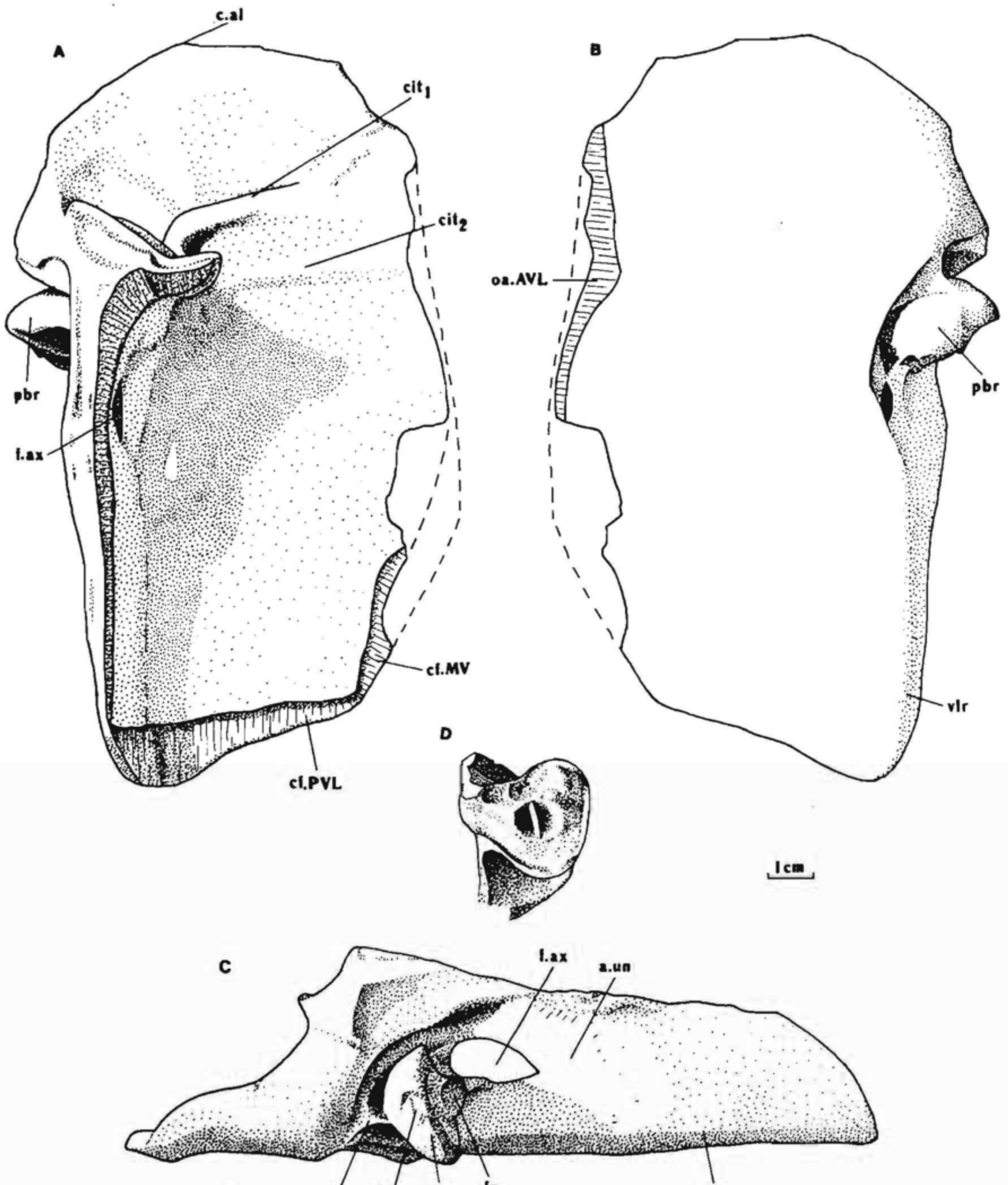
The median ventral plate (pl. 20 E) is of typical rhombic shape, the length/breadth index is about 1.4-1.7.

The pectoral fin (pl. 20, fig. C; pl. 21; text-figs. 19, 20) is represented by many disarticulated bones, and two specimens showing articulated plates of the proximal segment associated with the fragments of the AVL plate. There are three examples of the distal

Text-fig. 18. *Bothriolepis ornata* Eichwald. A-C, AVL plate LDM 100/414. A, visceral view. B, ventral view. C, lateral view. D, processus brachialis LDM 100/365. Skujaine River near Klūnas, Latvia. Tērvete Formation. x 0.7.

Text-fig. 19. *Bothriolepis ornata* Eichwald. Proximal segment of the pectoral appendage LGI 5/2050A. A, dorsal view. B, ventral view. Skujaine River near Klūnas, Latvia. Tērvete Formation.

Text-fig. 20. *Bothriolepis ornata* Eichwald. A, B, Cv_1 plate LDM 100/422 in dorsal and ventral view. C, Cv_1 plate LDM 100/421 in dorsal view. D, Cd_1 plate LDM 100/419 in dorsal view. E, Cd_1 plate LDM 100/418 in dorsal view. F, Cd_1 plate LDM 100/417 in dorsal view. G, Cd_2 plate LDM 100/424 in dorsal view. H, I, distal segment of the pectoral fin LDM 100/45 in ventral view and dorsal view. Skujaine River near Klūnas, Latvia. Tērvete Formation.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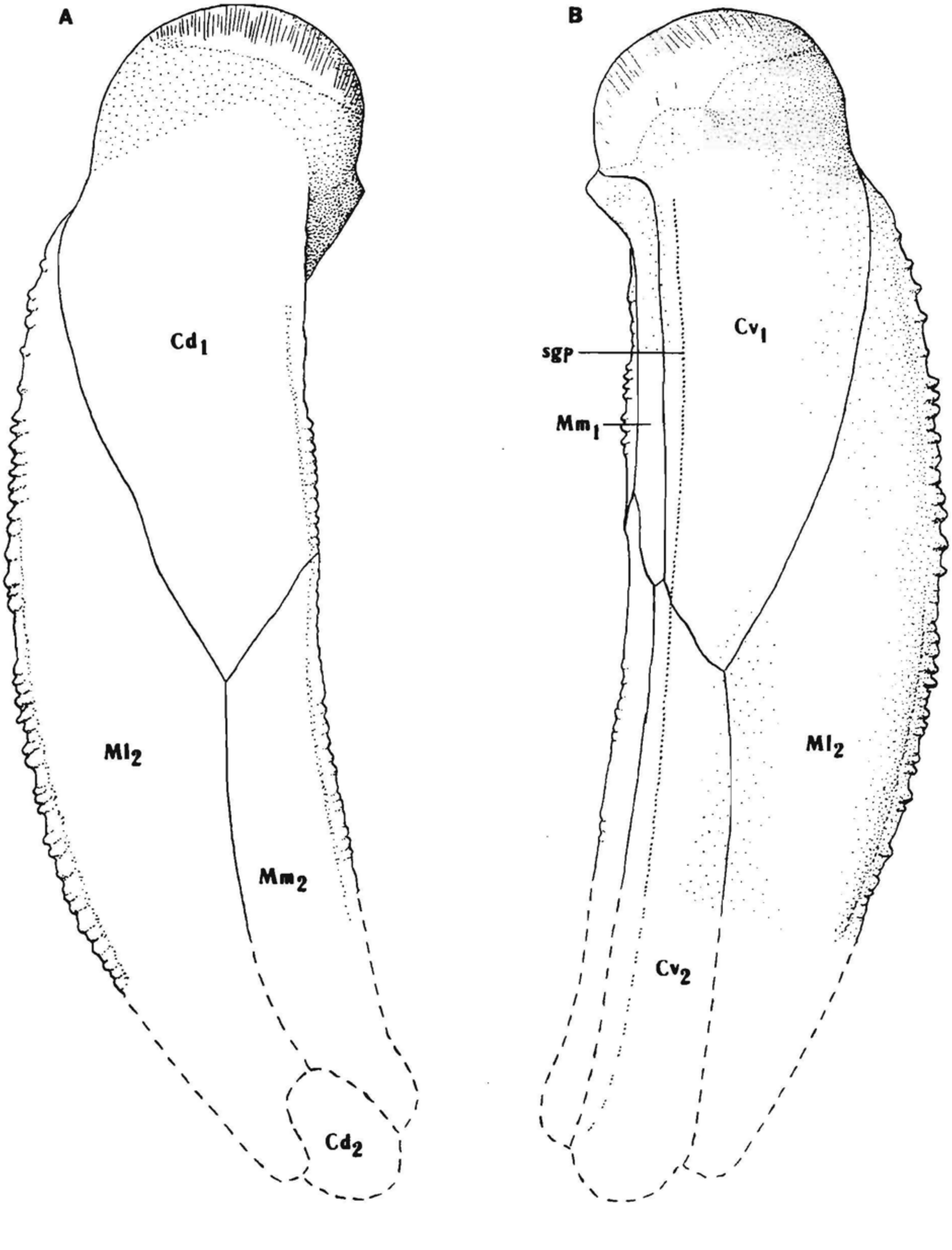
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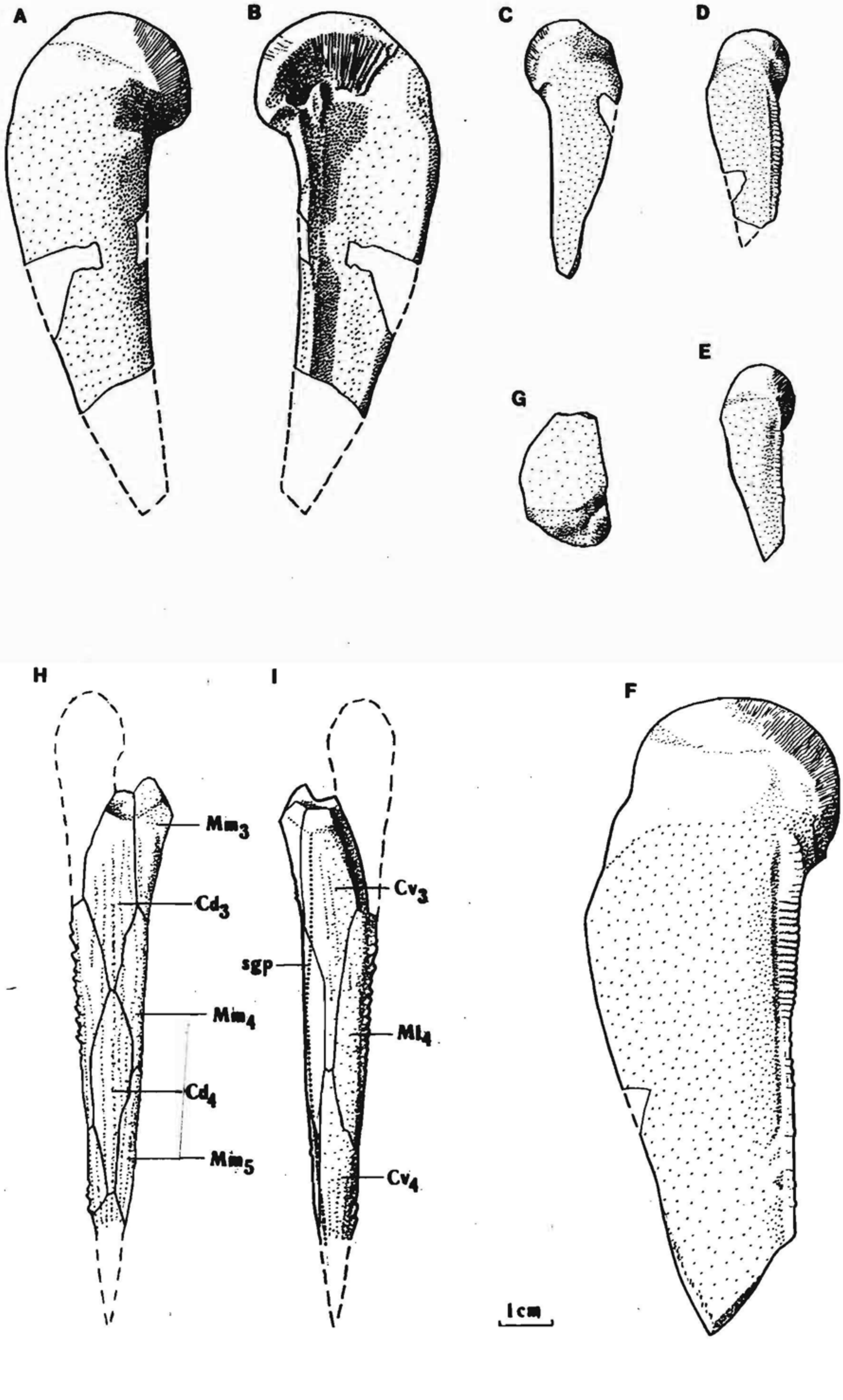
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segments. The proximal segment is of moderate length and is approximately 4 times as long as it is broad. Both segments bear prominent lateral and mesial spines. The spines are large and closely setting on the proximal segment, in large individuals 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 Mm_2 plate as in *B.canadensis*, but on the Cv_1 and Cv_2 plates similar to *B.cristata* Traquair. Than the pectoral pit-line groove continues on the distal segment. The lateral spines of the distal segment are sharp and proximally directed, the mesial margin bears few rounded tubercles. The Cd_1 is of moderate size with length/breadth index about 2.7. The Cv_1 is longer than the Cd_1 and slightly more elongate (L/B 3.1). The Cd_2 is slightly longer than broad. The Cv_2 is 4.5-5.1 times as long as it is broad. The distal segment is normally developed, Cd_3 and Cd_4 can be seen, Cd_5 is not present.

The ornamentation is typically reticulate, in quite large individuals becoming coarser and sparser. The network of anastomosing ridges is broken into irregular ridges, but never into short ridges or tubercles. The irregular ridges are situated without order, only one specimen of the PMD shows ridges, which are perpendicular to the margins of the plate. The ornamentation of the pectoral appendage remains reticulate even in quite large 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.

D i s c u s s i o n. The most part of described specimens gathered from the locality at Skujaine River downstream Klūnas hamlet, characterized by large amount of fish remains of several species. Except *Bothriolepis ornata* there are remains of other antiarch species *B.jani* Lukševičs (Lukševičs, 1986) found in the same layers of sand and sandstone. *B.ornata* can be distinguished readily from *B.jani* in its (1) larger size; (2) typical reticulate ornament, which is tubercular in *B.jani*; (3) shape and proportions of the almost all trunk-armour plates. *B.ornata* resembles *B.ciecere* Lyarskaja by some features (see the comparison with *B.ciecere*, p. 94).

Bothriolepis hayi Miles (1968) resembles *B.ornata* more than the other Scottish species of *Bothriolepis*. *B.ornata* differs from *B.hayi* most strikingly in the larger size and the narrower AMD and PMD plates, but also in the proportions of the Prm, La, Nu, Pn plates and more broad postnuchal ornamented corner of the ADL plate.

Among other species of *Bothriolepis*, *B.ornata* is morphologically closest to *B.groenlandica* Heintz (Stensiö, 1948). The two species are of similar size, and they resemble each other strikingly in the proportions and shape of almost all the head shield, trunk armour and pectoral fin 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 plates are narrower; (3) the rostral margin of the La plate is shorter; (4) the mesial division of the Pn plate is of different shape. It seems likely the above mentioned distinctions between *B.ornata* and *B.groenlandica* could be explained mostly by the intraspecific variation or preservation degree, but the solution of this problem needs to make reexamination of *B.groenlandica* and comparison of specimens from both Baltics and Greenland.

Bothriolepis jani Lukševičs, 1986

Plate 12; Text-figs. 21-24

Bothriolepis grossi: Lyarskaya, 1981, p.377 (nomen nudum).
Bothriolepis jani: Lukševičs, 1986, p.131, pl.1; text-figs.1,2.

H o l o t y p e. Right mixilateral plate LDM 100/88.

D i a g n o s i s. Small *Bothriolepis* with a median dorsal armour length of about 65 mm. Breadth/length index of trunk armour about 90. Praemedian plate broad, posterior margin is slightly shorter than almost stright anterior margin. Nuchal plate is strongly arched, short and broad, length/breadth index of 59. AMD is strongly arched, relatively broad, breadth/length 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 the posterior margin of the plate. Proximal segment of the pectoral appendage is of moderate breadth, 3 times as longs as it is broad, bears large 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.

M a t e r i a l. LDM 100/66-108, 100/119-122, 100/137, 100/148, 100/374-377, 100/431-434 (disarticulated plates of the trunk shield); 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 plates); 100/369, 100/428 (2 La plates); 100/429, LGI 5/2028 (2 Pp plates); LDM 100/138-143, 100/372, 100/430 (8 Nu plates).

L o c a l i t i e s. The type locality is exposure of white and pink sands containing abundant fish bones, dolomite marls and marls at the right bank of Skujaine River down Klūnas village. Other material comes from an outcrop of red and pink sandstones at the right bank of Svēte River near Ķurbes hamlet.

H o r i z o n. Holotype and the most part of material (collection LDM 100 and LGI 5/2028) came from the Upper Famennian Tērvete Formation of Latvia. Some specimens came from the Mūri Formation.

D e s c r i p t i o n. This species is represented only by disarticulated plates and single articulated proximal segment of the pectoral fin. Of the referred head shield plates only two

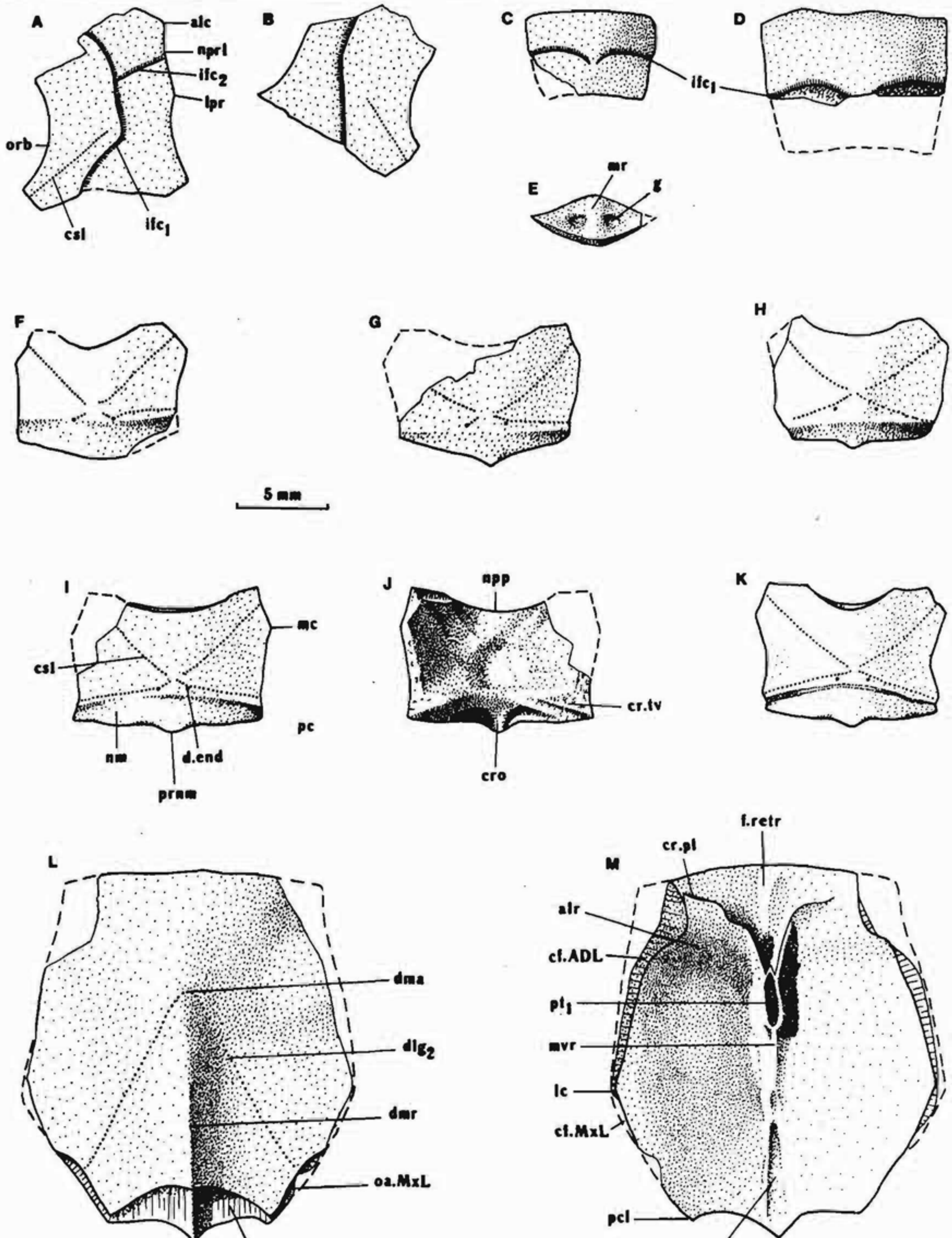
Prm, one La, two Pp and six Nu plates shows significant morphological features. LDM 100/144 is an anterior division of the Prm plate (pl. 12, fig. A; text-fig. 21 D), which is moderately arched with almost straight rostral margin. LDM 100/427 (text-fig. 21 C) is a more complete Prm plate. It is smaller than 100/144, more arched, broadest at the almost straight rostral margin. The orbital margin is not preserved, but the configuration of the praeorbital recess ventral wall suggests the Prm plate is much broader then it is long with the orbital margin slightly shorter than the rostral margin. The infraorbital sensory groove crosses the plate in its middle part. The anterior section of the supraorbital sensory line (soc) is not recognized.

LDM 100/428 is an incomplete La plate (text-fig. 21 B) exhibiting the posterior division with typical tubercular ornament. LDM 100/369 (pl. 12, fig. B; text-fig. 21 A) is almost complete La plate prepared from both sides. This lateral plate is moderately broad with length/breadth index of 136. The rostral margin as it is preserved is of moderate breadth and almost straight. There are well defined antero-lateral corner (alc) and the shallow prelateral notch (nprl). The infraorbital sensory groove crosses the plate in its middle part far from the orbital and lateral margins. The central sensory line groove (csl) usually is finished slightly anteriorly the level of the middle of orbital fenestra length. The semicircular pit-line groove (cir) and branch of infraorbital sensory line diverging on La (ifc_2) are well defined. Shape of the orbital margin shows the orbital fenestra is very large. The antero-lateral corner of otico-occipital depression (pr.po) on the visceral surface is relatively narrow and extends forward at the level of the middle of orbital fenestra length. The transverse lateral groove (tlg) is moderately broad and clearly defined.

The postpineal plate (LDM 100/429 and LGI 5/2028: pl. 12 , fig. C; text-fig. 21 E) is very broad, about twice as broad as it is long. The anterior margin is strongly convex. The median ridge (mr) sharing the deep paired pits (g) on the visceral surface of the plate is narrow. Both specimens clearly differs from the Pp plate of similar size LDM 100/373 from the same locality, which belongs to *B.ornata*, in their tubercular ornament and broader general proportions.

The nuchal plate (pl. 12 D, G; text-fig. 21 F-K) is strongly arched with an angle between right and left halves about 103-125°. It is relatively short and broad with a length/breadth index 57-63, 59 on the average. The plate is broadest across the lateral corners.

Text-fig. 21. *Bothriolepis jani* Lukševičs. A, B, incomplete La plates in dorsal view. A, LDM 100/369. B, LDM 100/428. C, D, Prm plates in dorsal view. C, LDM 100/427. D, LDM 100/144. E, postpineal plate LDM 100/429 in visceral view. F-K, Nu plates. F, LDM 100/140 in dorsal view. G, LDM 100/143 in dorsal view. H, LDM 100/142 in dorsal view. I, J, LDM 100/372 in dorsal and visceral view. K, LDM 100/430 in dorsal view. L-M, AMD plate LDM 100/67 in dorsal and visceral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation.


A
B
C
D
E
F
G
H
I
J
K
L
M
alc
nprl
ifc2
lpr
orb
csl
ifc1
mr
g
5 mm
mc
pc
nm
d.end
prnm
npp
cr.tv
cro
dma
dlg2
dmr
oa.MxL
oa.PMD
f.retr
cr.pl
alr
cf.ADL
pt1
mvr
lc
cf.MxL
pcl
grm

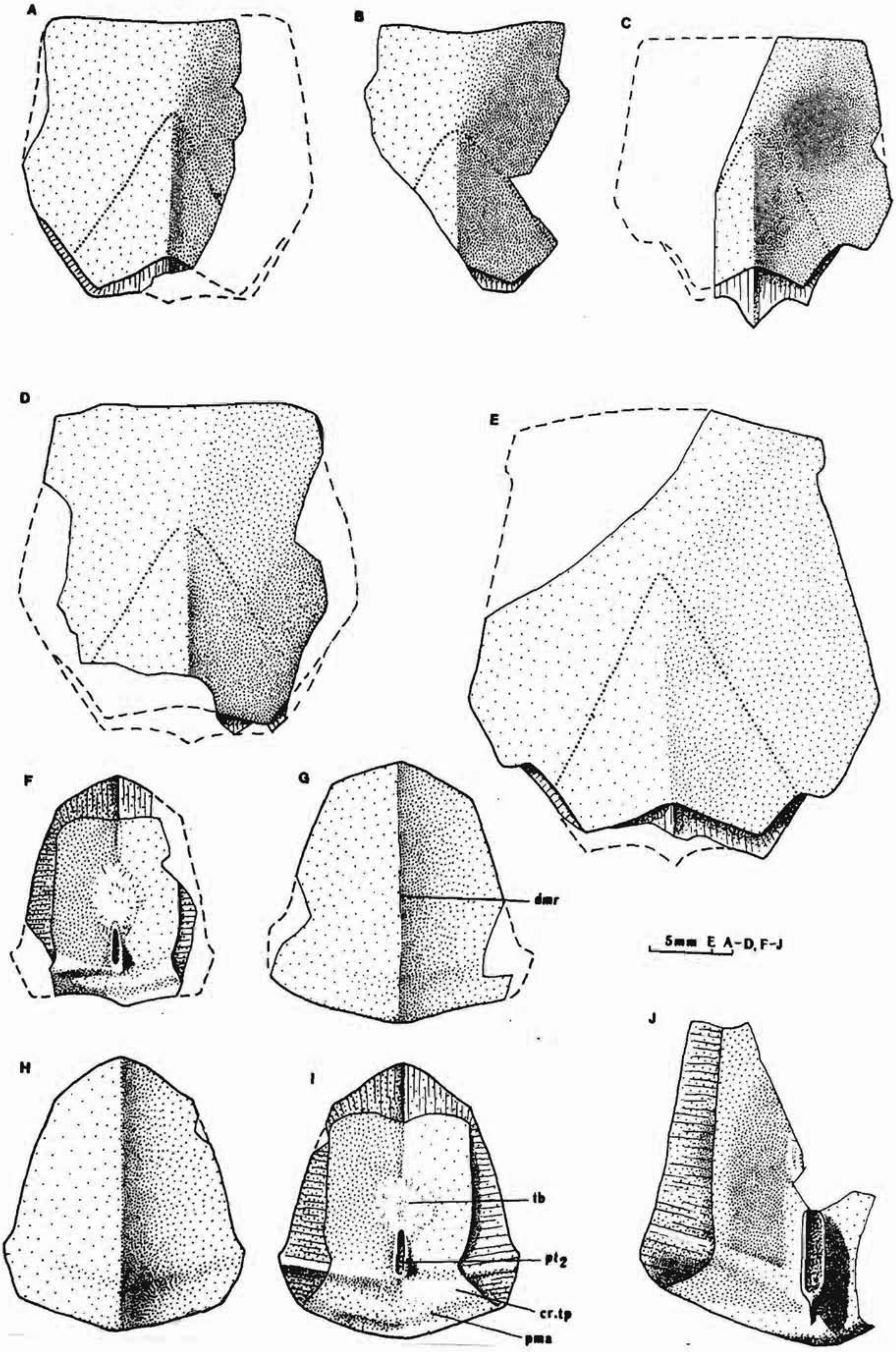
The anterior division of the lateral margin is much shorter than the posterior division. The posterior margin is slightly convex, it always bears the posterior process (mppr). The obtected nuchal area (nm) is relatively long, it probably extends on the Pn plate. The central sensory line groove is clearly distinct. In specimens LDM 100/140, 100/372 (pl. 12, fig. G) there are short supraoccipital grooves (socc), which terminate little in front of the obtected nuchal area at the large external openings for the endolymphatic ducts (d.end_2). Specimens LDM 100/141, 100/142, 100/430 (pl. 12, figs. F, D, E) show well defined supratemporal pit-line grooves (socc), which are not connected with d.end_2 and extends to the lateral margin of the plate. The postorbital crista (cr.pto) on the visceral surface is weakly developed. The median occipital crista (cr.o) and transverse nuchal crista are well defined. The postorbital ridge (cr.pto) can be recognized only in LDM 100/372 as a sharp transversely directed crest binding the orbital facets posteriorly.

The trunk-armour is relatively broad, breadth/length index 90. It is relatively low, with a lateral wall less than 3 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^o. The dorsal and lateral walls enclose an angle 120^o in the MxL plate and about 125-130^o in the ADL plate. 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 anterior median dorsal plate (pl. 12, figs. H-J; text-figs. 21 L, M; 22 A-E) is relatively broad, breadth/length index about 97, in large individuals it is broader than long. The plate is strongly arched, with right and left laminae forming an angle at the level of lateral corners of about 115^o 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 antero-lateral and lateral corners are rounded, but well developed, the postlevator processes are weakly defined. The posterior division of the lateral margin is slightly shorter than the anterior division. The tergal angle (dma) is situated posteriorly the anterior third of the plate and 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*. The posterior (dlg_2) oblique dorsal sensory line grooves are well defined.

The visceral surface of the AMD (text-fig. 21 M) shows a broad levator fossa (f.retr), which is limited by the low postlevator thickenings (alr) and strongly developed postlevator crests (cr.pl) with pronounced kink. The anterior edge of the crest do not reach a distinct, but

Text-fig.22. *Bothriolepis jani* Lukševičs. A-E, AMD plates in dorsal view. A, LDM 100/68. B, LDM 100/71. C, LDM 100/74. D, LDM 100/119. E, LDM 100/431. F-J, PMD plates. F, LDM 100/84 in visceral view. G, LDM 100/80 in dorsal view. H, I, LDM 100/83 in dorsal and visceral view. J, LDM 100/524 in visceral view. A-I, Skujaine River near Klūnas village, Latvia. Tērvete Formation. J, Svēte River near Ķurbes hamlet, Latvia. Mūri Formation.


A
B
C
D
E
F
G
H
I
J
dmr
5mm E A-D, F-J
tb
pt2
cr.tp
pma

narrow supranuchal area. The anterior ventral pit (pt_1) is elongated and deep, the median ventral ridge and groove (mvr, grm) are similarly developed as in *B. canadensis*.

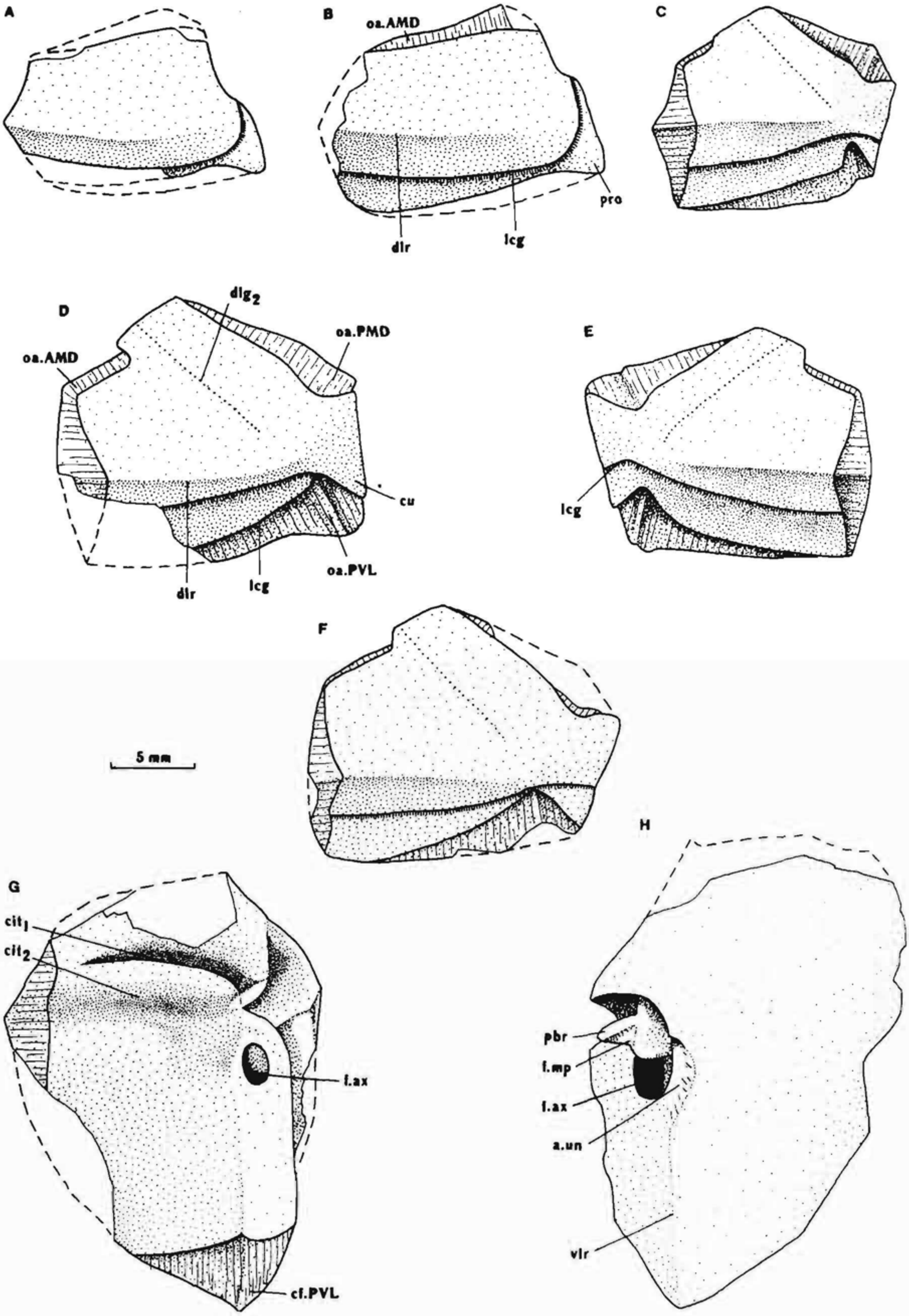
The posterior median dorsal plate (pl. 12, figs. K, L; text-figs. 22 F-J) is arched, moderately broad, breadth/length index about 87-104, bears well developed median dorsal ridge. The posterior margin is slightly convex, sometimes with weakly pronounced posterior corner. The width of the anterior margin comprises about 54% of total breadth. The lateral and postero-lateral corners are well defined. The visceral surface of the plate shows the well defined median ventral groove and distinct ventral tuberosity. The deep posterior ventral pit (pt_2) is positioned immediately in front of the transverse posterior crista (cr.tp).

The anterior dorsal lateral plate (pl. 12, figs. M, N; text-figs. 23 A, B) is moderately broad. The dorsal lamina is relatively narrow and long, and it's breadth a little exceeds height of the lateral lamina. Dorsal and lateral laminae of the plate enclose 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 postnuchal ornamented corner (pnoa) is weakly defined and stright.

The dorsal lamina of the mixilateral plate (pl. 12, fig. O; text-figs. 23 C-F) is moderately broad, less than twice as long as it is broad. The dorsal lamina is 1.7 times as broad as the lateral lamina is high. Dorsal and lateral laminae enclose 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 overlap area for the AMD is restricted to half the length of the antero-dorsal margin as in *Remigolepis* (Stensio, 1931). The posterior oblique sensory line groove (dlg_2) terminates some distance from the lateral margin. 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 anterior ventral lateral plate (pl. 12, figs. P, R; text-figs. 23 G, H) 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. The 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 (cit_1) running mesially subparallel to the low and broad transverse thickening (cit_2). Cit_1 terminates some distance from the mesial margin of the AVL.

Text-fig.23. *Bothriolepis jani* Lukševičs. A, B, ADL plates in dorsal view. A, LDM 100/121. B, LDM 100/122. C-F, MxL plates in dorsal view. C, LDM 100/432. D, LDM 100/87. E, holotype LDM 100/88. F, LDM 100/90. G, H, AVL plates. G, LDM 100/102 in visceral view. H, LDM 100/433 in ventral view. Skujaine River near Klūnas village, Latvia. Tērvete Formation.


A
B
C
D
E
F
G
H
oa.AMD
pro
dlr
lcg
dlg2
oa.PMD
cu
oa.PVL
5 mm
cit1
cit2
f.ax
cf.PVL
pbr
f.mp
a.un
vlr

There are two complete posterior ventral lateral plates LDM 100/434 (pl. 12, fig. S; text-fig. 24 A) and LDM 100/375. In LDM 100/434 it is of moderate breadth, the ventral lamina is 2.1 times as long as it is broad. The subanal division is relatively broad and short, it occupies only 17.7 of the total PVL plate length. The lateral lamina is of moderate height, 2.6 times as long as it is high. The ventral lamina is 1.5 times as broad as the lateral lamina high. The ventral and lateral laminae enclose the angle about 112^{o}. The ventro-lateral ridge (vlr) is well developed.

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

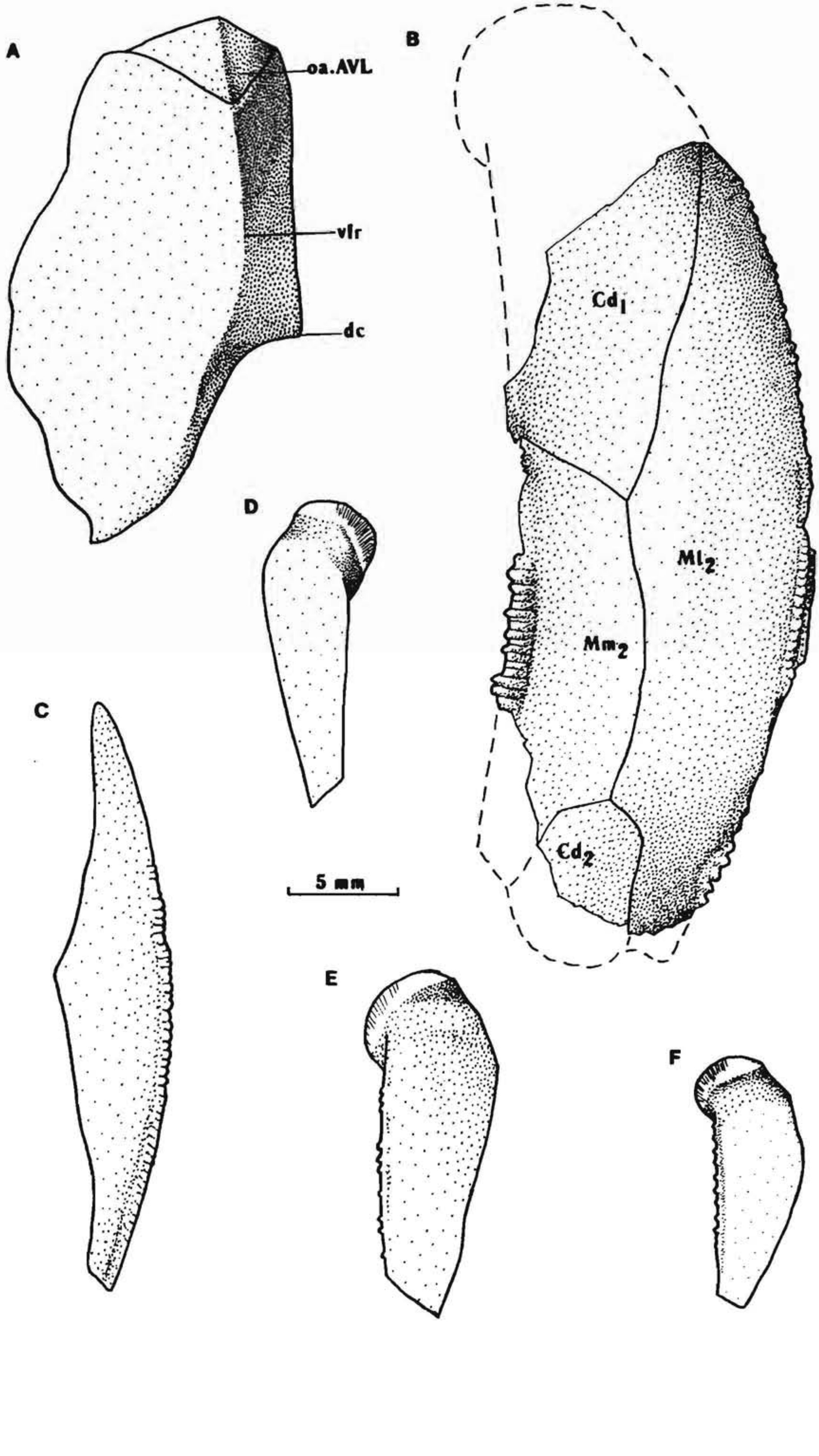
The pectoral fin is represented mostly by disarticulated bones, and specimen LDM 100/435 (pl. 12, fig. T; text-fig. 24 F) showing articulated plates of the proximal segment without the most proximal part. The proximal segment bears large prominent lateral and mesial spines. It is of moderate breadth, about 3 times as long as it is broad. The Cd_1 is of moderate size with length/breadth index varying from 2.8 to 3. The Cv_1 is longer than the Cd_1 and slightly more elongated (L/W=3.3). The Ml_2 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 long on the Prm and short on most of the other plates. Along the obtected nuchal area on the Nu plate and posterior margin of the lateral lamina of the PVL tubercles may fuse into the ridges. More regular setting of tubercles is recognized on the proximal segment of the pectoral fin.

R e m a r k s. *B.jani* differs from most of other *Bothriolepis* by its typical tuberculate ornament, which is similar to that of *Grossilepis tuberculata* (Gross) and *G.spinosa* (Gross). *B.jani* differs from *G.tuberculata* in its (1) shape and proportions of the PMD, MxL and PVL plates; (2) sutural connections of the AMD and MxL; (3) shape of the postnuchal ornamented corner of the ADL; (4) smaller axillary foramen; (5) proportions of pectoral fin bones.

D i s c u s s i o n. The most part of described specimens gathered from the locality at Skujaine River downstream Klūnas village, characterized by large amount of fish remains of several species. Except *Bothriolepis jani* there are remains of other antiarch species *B.ornata* found in the same layers of sand and sandstone. A comparison of *B.jani* with *B.ornata* could be found at the end of description of *B.ornata*.

Text-fig.24. *Bothriolepis jani* Lukševičs. A, PVL plate LDM 100/434. B, proximal segment of the pectoral appendage LDM 100/435. C, Ml_2 plate LDM 100/378. D, Cv_1 plate LDM 100/134. E, F, Cd_1 plates. E, LDM 100/130. F, LDM 100/133. Skujaine River near Klūnas village, Latvia. Tērvete Formation.


A
oa.AVL
vlr
dc
B
Cd1
Ml2
Mm2
Cd2
D
C
5 mm
E
F

B.jani can be distinguished readily from the other Famennian *Bothriolepis* representatives of similar or slightly larger size *B.ciecere* Lyarskaja, *B.cristata* Traquair and *B.hydrophila* (Ag.) (Miles, 1968) by its typical tuberculate ornament, which is similar to that of *Grossilepis tuberculata* and *G.spinosa*. *B.jani* differs well from *B.nielseni* Stensio (1948) in absence of a crest on the dorso-lateral ridge. *Bothriolepis* sp.nov., described by Gross (1942) from the locality at Svēte River resembles *B.jani* in its tubercular ornament but differs in absence of the ventro-lateral ridge on the PVL. The species *B.jani* and *B.lohesti* Leriche from Belgium are clearly close morphologically. They are similar in (1) the shape and proportions of the AMD; (2) sutural connections between the AMD and MxL. Unfortunately, *B.lohesti* is represented by a few remains of the AMD, ADL and pieces of the pectoral fin bones and it does not allow to compare both species with sufficient detail. The distinctions between the two species are insignificant and consist in that in *B.lohesti* (1) the AMD is less arched; (2) ornament consists of tubercles and nodose ridges. It seems likely that *B.jani* and *B.lohesti* are phylogenetically very close.

Bothriolepis heckeri sp.nov.

Plate 6, figs. K-M; Text-figs. 25 A-E

H o l o t y p e. Anterior median dorsal plate PIN 835/42.

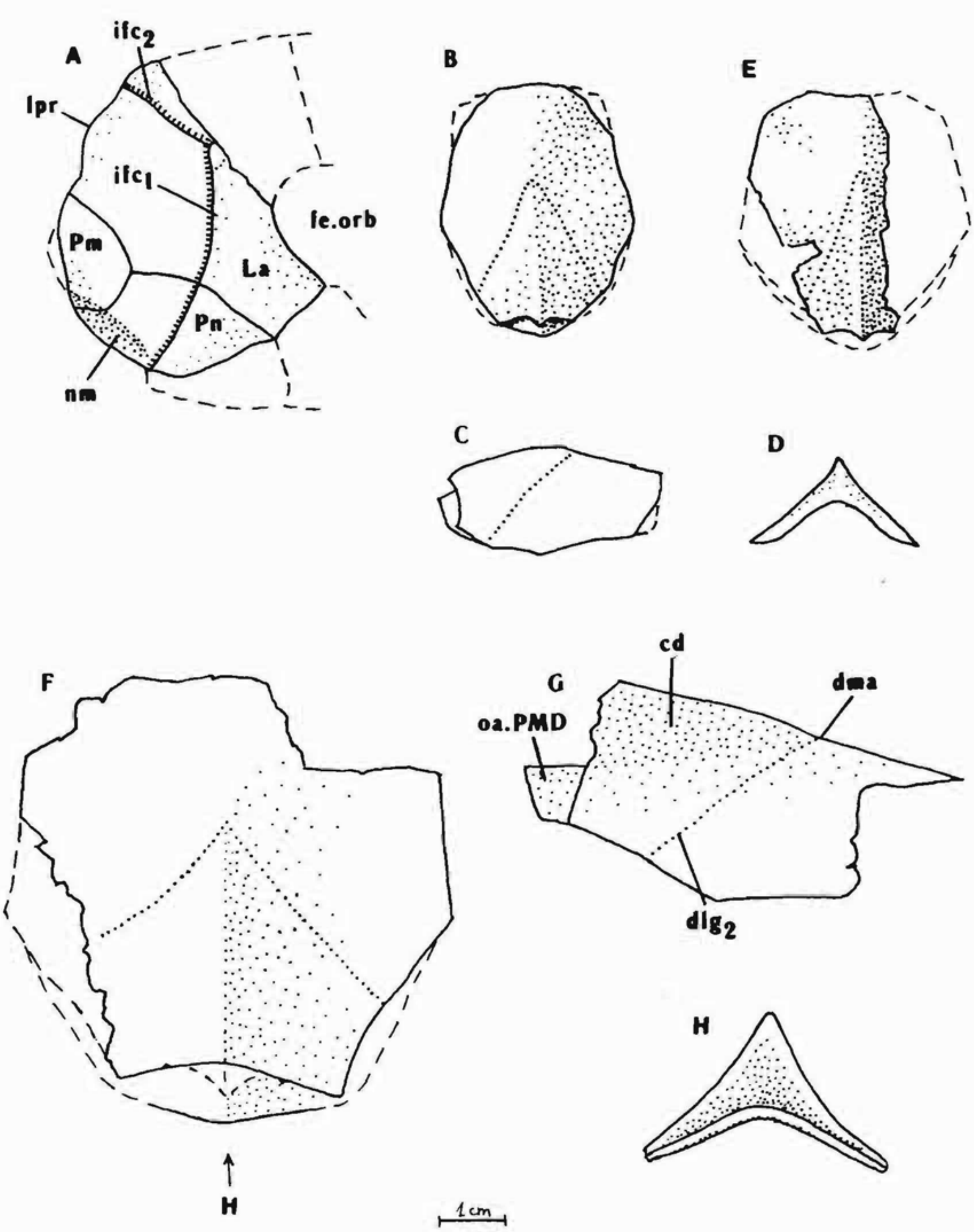
D i a g n o s i s. Moderately large *Bothriolepis* with comparatively narrow and strongly arched AMD (breadth/length index of about 81) which bears high dorsal median crest arising just before the tergal angle. La plate is broad with very long infraorbital sensory groove diverging on La.

M a t e r i a l. PIN 835/41, an incomplete AMD; PIN 835/40, an incomplete La, Pn and Pmg; all gathered by R.Hecker in 1930.

L o c a l i t y. Outcrops at the right bank of Malyy Tuder River not far from Bilovo village, Novgorod region, Russia.

H o r i z o n. Bilovo Beds (?), Famennian.

D e s c r i p t i o n. PIN 835/42 is a relatively small almost complete AMD with damaged antero-lateral corners and PIN 835/41 is an imperfect AMD without the right lateral margin and loosed the left postero-lateral margin. The AMD plate is comparatively narrow with breadth/length index of about 81, with a gently concave anterior margin, which is moderately broad. The posterior margin is relatively narrow, about 1.2 times shorter that the anterior margin. The AMD plate is strongly arched with the angle between the two laminae reaching about 100^{o}, and bears a comparatively high dorsal median crest (cr.d) which arises just before the tergal angle. The antero-lateral angle is weakly defined. The



Text-fig. 25. A-E, Bothriolepis heckeri sp.nov. A, incomplete La, Pn and Pmg plates PIN 835/40. B-D, holotype, AMD plate PIN 835/42. B, dorsal view. C, lateral view. D, anterior view. E, incomplete AMD plate PIN 835/41 in dorsal view. F-H, Bothriolepis sp.indet.1, AMD plate in dorsal, lateral and posterior view, respectively. A-E, Malyy Tuder River not far from Bilovo village, Novgorod region, Russia. Bilovo Beds (?). F-H, Msta River in between Solodka and Navolok villages, Novgorod region, Russia. Famennian.

tergal angle (dma) is situated slightly posteriorly the anterior third of the plate length. The posterior oblique dorsal sensory line grooves (dlg_2) are well defined. The ornament of the reticular type, sometimes with slightly defined ridges.

PIN 835/40 is an incomplete head-shield consisting of an incomplete La plate which lacks the margin making contact with the Prm plate, articulated with the anterior portion of the left Pn plate and almost complete Pmg plate. 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 orbital fenestra length. The branch of the infraorbital sensory groove diverging on La (ifc_2) is well defined and unusually long. The Pn plate seems to be relatively broad as it is preserved. The Pmg plate of unusual shape with median margins longer that the lateral margins.

D i s c u s s i o n. *Bothriolepis heckeri* sp.nov. differs well from all the other known *Bothriolepis* from the Main Devonian Field in its broad La with unusually situated sensory grooves. It resembles *Bothriolepis* sp.indet.1 in the strongly developed dorsal median crest on the AMD plate, but differs well in general proportions of this plate. *Bothriolepis heckeri* resembles *Bothriolepis cristata* Traquair (Miles, 1968) from the Rosebrae Beds of Scotland in a presence of a strongly developed dorsal median crest on the dorsal wall of the trunk armour, but differs in other shape and general proportions of the AMD plate.

Bothriolepis ciecere Lyarskaja, 1974

Plates 22; 23, figs. A-J; 24; 25

Bothriolepis ornata Eichw.: Gross, 1933, S.41.
Bothriolepis cf. *ornata* Eichw.: Gross, 1942, S.421-422, abb.2.
Bothriolepis cf. *ornata* Eichw.: Lyarskaya, Savvaitova, 1974, p.97.
Bothriolepis ciecere: ibid., p.99, pl.I, figs.1-4; text-figs.5-8.
Bothriolepis pavariensis: ibid., p.104, pl.I, figs.5-7; text-figs.9-10.
Bothriolepis ciecere Lyarskaja: Lukševičs, 1991, p.39-47, pl. 1-3, text-figs.1-8.

H o l o t y p e. Anterior median dorsal plate LDM 43/303.

D i a g n o s i s. Rather large *Bothriolepis* with a median dorsal armour length of at least 200 mm. Dorsal wall of moderate width. Breadth/length index of trunk armour about 77. Breadth/length index of the head-shield of 120. Anterior margin of the head-shield is rounded. Orbital fenestra is not large. Praemedian plate broad, posterior margin is slightly shorter than anterior margin. Nuchal plate is strongly arched, moderately broad, length/breadth index of

80. AMD is moderately broad, breadth/length index 87. Anterior part of AMD is arched, posterior part is flat. Posterior margin of AMD and anterior margin of PMD are very narrow. Median dorsal ridge poorly developed. Dorso-lateral and ventro-lateral ridges are well marked, dorso-lateral ridge bears smooth tubercles. Dorsal and lateral walls of trunk enclosing an angle of 125^{o} on ADL and 111^{o} on MxL. Lateral and ventral walls enclosing an angle of 101^{o}. Proximal segment of the pectoral appendage is moderately long, 3.5 times as longs as it is broad. Ornamentation typically reticulate, in quite large individuals becoming coarser and sparser.

M a t e r i a l. 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.

L o c a l i t i e s. The type locality is outcrop exposing the light-coloured sands, sandstones, siltstones, clays and dolomite marls at the left bank of Ciecere River downstream from the Pavāri hamlet. Other material comes from an outcrop exposing light sands and sandstones at the right bank of Venta River 1 km W from Ketleri hamlet.

H o r i z o n. All material from the type locality came from the uppermost Upper Famennian, the middle Member (Airītes) of the Ketleri Formation (Savvaitova, 1977). Other material is from the upper Member (Varkaļi) of the Ketleri Formation.

D e s c r i p t i o n. This species is very well represented at the two localities: at the right bank of Venta River 1 km W from Ketleri hamlet and at the left bank of Ciecere River downstream from the Pavāri hamlet by many disarticulated plates and some articulated skulls. Most are from well-grown individuals of moderate size, but there are also some quite large specimens. The head-shield (pl. 22, figs. A, B) is of moderate size, breadth/length index is about 120. The head-shield 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 antero-lateral corners (alc) and the deep prelateral notch (nprl). The obtected nuchal area (nm) is short, broadest on the Nu plate, with slightly defined lateral and median processes. The orbital fenestra is relatively small, with a breadth/length index about 190. Preorbital recess (prh) is distinctly trifid with extended lateral horns and a pointed median division.

The visceral skull surface shows the normal features. The broad otico-occipital depression (ood) is well defined by the paramarginal cristae (cr.pm). The antero-lateral corner of the otico-occipital depression (pr.po) is broad in its base, postero-lateral corner is rounded and extends laterally over the middle of the Pn plate's posterior margin. The transverse lateral groove (tlg) is moderately broad and clearly defined. A broad shallow depression anteriorly from the antero-lateral corner of the praeorbital recess is the lateral pit (p), which is situated equally spaced from an orbital edge of the La plate and prelateral notch. The median occipital crista (cr.o) is slightly defined, often it consists of several radially arranged small ridges. The transverse nuchal crista is prominent. The median ridge (mr) sharing the deep paired pits (g) of the Pp plate is low in large individuals and in individuals of moderate size it is defined as a tubercle in front of the groove connecting the pits.

The praemedian plate is relatively broad, breadth/length index 94-118. It is broadest at the infraorbital sensory groove or rostral margin. A rostral angle (ac) is present on the half of large individuals. The rostral and orbital margins are convex, orbital margin is only slightly shorter than the rostral margin. The orbital margin bears slight nasal notch (pnn). The infraorbital sensory groove crosses the plate in its middle part. 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 praeorbital recess.

The lateral plate is moderately broad with length/breadth index 136 on the average (pl. 22, figs. C, D). The rostral margin is of moderate breadth and almost straight, the antero-median and antero-lateral corners are well defined. The infraorbital sensory groove crosses the plate in its middle part far from the orbital and lateral margins. The central sensory line groove (csl) usually is finished at the level of the middle of orbital fenestra length. The semicircular pit-line groove (cir) and branch of the infraorbital sensory line diverging on La (ifc_2) are well defined.

The pineal plate (pl. 22, figs. H-J) is known only from the Ketleri locality. It is relatively broad, breadth slightly exceeds a length. The postero-lateral corners are weakly defined. The anterior and lateral margins are concave, the posterior margin is slightly convex. There is a broad area without ornamentation (sp) along the posterior margin. A deep, but small pineal pit (pip) 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 postpineal plate is broad in small individuals and of moderate breadth in maturity, length/breadth index varies from 45 to 80. As in other species the anterior margin is strongly convex in small specimens and became almost straight with increasing size.

The nuchal plate (pl. 22 M-T) is vaulted with an angle between the right and left halves slightly larger than 130^{o}. It is moderately broad with a length/breadth index 68-93, 80 on the average. The plate is broadest across the lateral corners. The anterior division of the lateral margin usually is concave 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 the one side of the plate (LGI 5/2025; pl. 22, fig. P), interrupted or very short (LDM 57/14, 57/18, 57/723; pl. 22, fig. T). In some cases there are short supraoccipital grooves (socc), which terminate little in front of the obtected nuchal area at the rather large external openings for the endolymphatic ducts (d.end$_2$). Postorbital crista (cr.pto) on the visceral surface is low.

The paranuchal plate (pl. 22, figs. U, V) is of moderate width, length/breadth index 88-110. The lateral division of the Pn is relatively narrow and is composing 40-50% of the general breadth of a plate.

The postmarginal plate is relatively broad with the lateral margin slightly longer than the median margin.

The submarginal (extralateral) plate is known from one specimen, LDM 57/328. It is relatively short with a length/breadth index about 150. The dorsal margin has a prominent antero-dorsal process and posterior attachment area for the skull. The posterior margin is strongly convex, the ventral margin is weakly concave. A well marked lateral notch (n.la) is rather deep separating the plate into a short thick anterior division and more thin posterior division.

The trunk armour in individuals of moderate size is known from a large amount of isolated plates from the locality at Ciecere River near Pavāri hamlet, as well as from a part of the dorsal wall of the trunk armour prepared from visceral surface, consisting of AMD, PMD, left ADL and MxL (LDM 81/58-81/60) and several articulated bones from the same site. Plasticine reconstruction were used to describe the features of the trunk armour.

The trunk armour in individuals of moderate size is comparatively broad, breadth/length index 77. It is relatively low, with a lateral wall less than 3 times as long as high; in comparison with some other species rather flattened with a low dorsal wall. The length of the dorsal wall, probably, is more than 200 mm. The ventral wall is not quite flat, but slightly vaulted transversely. It is gently arched also in rostrocaudal direction in the posterior division of the armour. The median dorsal ridge is weakly defined. 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 anterior median dorsal plate (pl. 23, figs. A-H) is moderately broad, breadth/length 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 may be weakly concave or less often fairly straight in large individuals. It is moderately broad and 1.1-1.7 times as long as a narrow posterior margin. The antero-lateral and lateral corners are rounded, the postlevator processes are weakly defined. The posterior division of the lateral margin is 1.5-1.9 times shorter than the anterior division. The tergal angle (dma) is situated within the anterior third of the plate and is weakly marked. There is no median dorsal ridge. Overlap areas for ADL and MxL are normally developed as usually in *Bothriolepis*, but in LDM 43/5082 and 81/30 AMD overlaps the MxL by short anterior part of the posterior division of the lateral margin and in LDM 81/262 sutural connection of AMD with MxL is of *Remigolepis* type. The anterior (dlg_1) and posterior (dlg_2) oblique dorsal sensory line grooves are well defined only on the plates of individuals of small and moderate size. In many cases the posterior oblique dorsal sensory line grooves are 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 antero-laterally and terminates at the AMD/ADL suture (LDM 81/36, 81/371). The dlg_2 in 20% of the moderate size individuals are not present.

The visceral surface of the AMD (pl. 23, figs. E, H) shows a slightly lengthened levator fossa (f.retr), which is limited by the low postlevator thickenings (alr). The anterior ventral pit (pt_1) 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 the 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. AMD from the Ketleri locality differ a little from specimens, found at Ciecere River, by greater thickness.

The posterior median dorsal plate (pl. 23, figs. I, J; pl. 24, figs. A, B) is narrow, breadth/length index about 80-91, 86 on the average. It is almost flat in the anterior part and arched in the posterior part. The anterior and posterior margins both are strongly convex, in large individuals the posterior margin with pronounced posterior corner. The width of the narrow anterior margin varies between 37-44% of total breadth. The lateral and postero-lateral corners are well defined. The median dorsal ridge is present only in the posterior quarter of the plate. Specimen LGI 5/2023 (pl. 23, figs. I, J) shows the abnormally developed overlap area for the MxL, probably arisen as a result of damage of the living animal bone. 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 (pt_2) in large individuals. The crista transversalis interna posterior (cr.tp) is low and smoothed, the postmarginal area (pma) is rather broad.

The anterior dorsal lateral plate (pl. 24, figs. C-E) is slightly shorter than the mixilateral plate in articulated armour. The dorsal lamina is relatively narrow and long, and it's breadth a little exceeds height of the lateral lamina. Dorsal and lateral laminae of the plate enclosing an angle of 120-125^{o}. The dorso-lateral ridge (dlr) is well defined. The postnuchal ornamented corner (pnoa) is sharp, long and narrow. Specimen LDM 81/421 shows the dorsal overlap area partly overlapping the AMD plate.

The mixilateral plate (pl. 24, figs. F-K) is moderately long. The dorsal lamina of the plate is narrow, less than twice (1.8 on the average) as long as it is broad. Dorsal and lateral laminae enclosing an angle about 111°. The lateral lamina is moderately high, 2.9 times as long as it is broad. The posterior oblique sensory line groove (dlg_2) terminates in some distance from the lateral margin, almost in half of the specimens it is not present. In specimens LDM 81/211 and 81/406 there is an additional branch of the posterior oblique dorsal sensory line groove dlg_2', which is parallel to dlg_2. The dorso-lateral ridge is well defined and even in small individuals bears tubercles. 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 anterior ventral lateral plate (pl. 25, figs. F-J) is of moderate breadth, the ventral lamina is 1.7-2.2 times as long as it is broad. The subcephalic division is relatively short and 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 ventro-lateral ridge is well defined. The axillary foramen (f.ax) is rather large and rounded in shape. The visceral surface of the AVL shows the high transverse anterior crista (cit_1) running antero-mesially parallel to the low and broad transverse thickening (cit_2).

The posterior ventral lateral plate (pl. 25, fig. A-E) has similar proportions to the AVL, as in most *Bothriolepis* species. It is of moderate breadth, the ventral lamina is 2-2.6 times as long as it is broad. The subanal division is relatively broad and moderately long, it occupies about one fifth (18-22%) of the total PVL plate length. The lateral lamina is high, 1.8-2.4 times long as it is high. The ventral lamina only 1.1 times as broad as the lateral lamina high. The lateral lamina rather steep, the angle between laminae is about 101°. Similar to AVL 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 median ventral plate is typically developed, the length/breadth index is 1.3.

The pectoral fin 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 of moderate length and is 3.5 times as long as it is broad. The Cd_1 is of moderate size with length/breadth 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 pl. 25.

The ornamentation is typically reticulate, in quite large individuals becoming coarser and sparser. The network of anastomosing ridges are broken into shorter ridges on the anterior part of the La and Prm plates and in large specimens also on the Nu and Pp plates. The ornament on the Sm plate consists of short ridges and tubercles. The ornament on the plates of the trunk armour 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 the bones the anastomoses between the ridges reduce. On the AMD the ornament may consist of ridges parallel to margins of the plate, but on the MxL and PVL plates there are short ridges perpendicular to dorso-lateral or ventro-lateral ridge. The ornamentation of the pectoral appendage is more variable. It is reticulate in general, on the Cd_1 the ornament is radially arranged so that the perpendicular ridges are parallel to the mesial margin. The network ridges bear weak elevations in the points of anastomoses on the Ml_2 and Cv_1.

R e m a r k s. *Bothriolepis pavariensis* Lyarskaja was described as a new species which differs from *B.ciecere* in its (1) larger size; (2) broader Prm plate; (3) shape of the Pp plate; (4) size and position of the external openings for the endolymphatic ducts; (5) position and shape of a branches of the posterior oblique sensory line groove; (6) shape of the AMD plate (Lyarskaya, Savvaitova, 1974). Unfortunately the description was based on some poorly preserved specimens from the Pavari locality. 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 plates; or by considerable intraspecific variation characteristic of *B.ciecere*: the position and shape of the posterior oblique sensory line groove.

D i s c u s s i o n. *Bothriolepis ciecere* can be distinguished readily from *B.curonica* Gross (Lukševičs, 1987) and *B.jani* Lukševičs (Lukševičs, 1986), the other Famennian *Bothriolepis* representatives from the Main Devonian field, and resembles *B.ornata* Eichwald by some features. *B.ciecere* differs from *B.ornata* in its (1) smaller size; (2) shape and proportions of the Pn and Prm plates; (3) position of the lateral pit on the La plate and postero-lateral corner of the otico-occipital depression on the Pn plate; (4) broader anterior margin of the AMD plate; (5) shape of the PMD plate; (6) 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 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 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 the ornament.

The species *B.ciecere* and *B.nielseni* Stensiö from Greenland are clearly very close morphologically. They are similar in (1) the general proportions of the trunk armour; (2) the development of dorso-lateral ridge; (3) the shape and proportions of individual plates of the trunk armour; (4) the reticulate ornament. Unfortunately, *B.nielseni* is represented only by the holotype which consists of a crushed and flattened trunk armour and poorly preserved parts of the head-shield and pectoral fin (Stensiö, 1948). Absence of the description of the head-shield and 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 AMD is longer; (3) the proximal segment of the pectoral fin is more slender; (4) ventrolateral 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 stratigraphic situation, as well as fact, that both *B.ciecere* and *B.nielseni* are the youngest species, the last representatives of *Bothriolepis* in Greenland and Baltics respectively.

Bothriolepis sp.indet.1

Text-figs. 25 F-H

M a t e r i a l. PIN (unnumbered), an incomplete AMD; PIN (unnumbered), an incomplete PMD; both gathered by R.Hecker in 1929.

L o c a l i t y. Outcrops # 140 and 142 containing a light globular sandstone at the right bank of Msta River in between Solodka and Navolok villages, Novgorod region, Russia.

H o r i z o n. Famennian.

D e s c r i p t i o n. PIN is a moderately large incomplete AMD with preserved right lateral margin. It is comparatively broad as it is preserved, with the anterior and posterior margins seem to be relatively long. The AMD plate is strongly arched and bears a comparatively high dorsal median crest (cr.d) which arises at the tergal angle. The posterior oblique dorsal sensory line grooves (dlg_2) are well defined. PIN is an incomplete and laterally strongly flattened PMD plate, in which only the anterior and posterior margins, as well as a high dorsal median crest are partly preserved. The PMD plate bears a short posterior ventral pit on the visceral surface. *Bothriolepis* sp.indet.1 resembles *Bothriolepis cristata* Traquair (Miles, 1968) from the Rosebrae Beds of Scotland in the general proportions of the AMD plate and presence of a very sharply developed dorsal median crest on the dorsal wall of the trunk armour, but differs in its rather large size and other shape of the dorsal median crest. *Bothriolepis* sp.indet.1 slightly resembles *Bothriolepis obesa* Traquair (Miles, 1968) from the Upper O.R.S. of Roxburgshire in size, general proportions of the AMD plate and ornamentation, but differs in a more strongly developed median dorsal crest.

Bothriolepis sp.indet.2

Plate 23, figs. K, L

M a t e r i a l. LP 14/7, a Prm plate.

L o c a l i t y. Quarry and mines not far from Zarubino village approximately 25 km S-E from Lyubitino town, Novgorod region, Russia.

H o r i z o n. Famennian.

D e s c r i p t i o n. LP 14/7 is a relatively large Prm plate with typical reticulate ornamentation. It is unusually 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 times longer than the wavy orbital margin, which bears the clearly defined nasal notches. The infraorbital sensory groove (ifc_1) 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 praeorbital recess is of trifid type. The specimen LP 14/7 resembles the Prm plate of *Bothriolepis ciecere* in the nature of the ornament, general proportions and position of the supraorbital canal. However, it is more strongly arched and have different position of the infraorbital sensory groove. Compared to the Prm plate of *B.ornata*, it has similar ornament and position of sensory grooves, but differs in the proportions and vault.

Grossilepis Stensiö, 1948

T y p e s p e c i e s: *Grossilepis tuberculata* (Gross, 1941).

D i a g n o s i s. Bothriolepididae in which the AMD plate of an almost uniform breadth behind the postlevator processes, and normally overlaps both the ADL and MxL plates. The ADL and MxL plates also fairly uniform in width throughout their extent.

Grossilepis tuberculata (Gross, 1941)

Bothriolepis cellulosa (Pander): Gross, 1932, S.24 (in part).
Bothriolepis cellulosa (Pander): Gross, 1933, S.36-39, Taf.4, Fig.5 (in part).
Bothriolepis tuberculata: Gross, 1941, S.32-57, Abb.25,26A-G,27A-C, 28-43; Taf.18-28.
Bothriolepis cellulosa (Pander): Obruchev, 1947, Pl.LV, fig.4.
Grossilepis tuberculata (Gross): Stensiö, 1948, p.524-534, text-figs.26L, 28E, 35F, 36C-E, 39D, 41D, 43E, 44F, 45H, 47D, 48D, 53D, 266-271.

H o l o t y p e. AMD plate kept in SMNH (Gross, 1941, Abb.30F, Taf.21, Fig.1).

D i a g n o s i s. Relatively small bothriolepidoid with estimated length of dorsal wall of trunk shield reaching about 9 cm. Head-shield is moderately vaulted with anterior margin much shorter posterior margin. Postero-lateral corners of head-shield extends anteriorly to the level of the orbital fenestra posterior margin. Nu plate is of moderate width with length/breadth 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 plate with broad lateral division. Tergal angle is situated between the anterior and middle thirds of the AMD length. Dorsal median ridge is normally developed from the tergal angle backwards to the posterior corner of PMD plate. AMD plate is narrow with breadth/length index about 69-79. Posterior margin very broad. Lateral corner is slightly pronounced or sometimes even not be clearly identifiable. PMD plate is of moderate breadth with breadth/length index varying from 81 to 101. Pectoral fin is fairly slender, proximal segment from 4.5 to slightly more than 5 times as long as it is broad. Lateral spines of the pectoral fin are numerous, small, closely set and obtuse. Ornament consists of numerous closely and irregularly set pointed tubercles in well-grown individuals.

M a t e r i a l. LDM 65/77: MxL; NHM 17827: La, NHM 17811, 17817, 17820: three PMD plates, NHM 17812: PVL plate.

L o c a l i t i e s. The type locality is an outcrop of dolomites, dolomite marls and clays at the right bank of Daugava River near Koknese, Latvia.
H o r i z o n. The Lower Frasnian Pļaviņas Regional Substage, from Snetnaya Gora to Chudovo Beds.
R e m a r k s. This species is well described by Gross (1941) and Stensiö (1948) and therefore its description is not repeated here.

Grossilepis spinosa (Gross, 1942)

Bothriolepis spinosa: Gross, 1942, S.418-420, Abb. 9 A-D.
Grossilepis (?) *spinosa* (Gross): Stensiö, 1948, p.615.

H o l o t y p e. Nu plate kept in SMNH (Gross, 1942, Abb.9A).
D i a g n o s i s. A small bothriolepidoid with estimated length of dorsal wall of trunk shield reaching about 6 cm. Nu plate is moderately wide with length/breadth index of 62 in holotype, with convex posterior margin bearing the sharp median process, shallow postpineal notch on the anterior margin, slightly pronounced postero-lateral corners and well defined lateral corners. AMD plate is moderately broad with estimated breadth/length index 77. Clearly defined lateral corner is slightly pronounced. Lateral spines of Ml_2 are strikingly long and pointed. Ornament consists of numerous closely and irregularly set tubercles.
M a t e r i a l. The specimens described and illustrated by Gross (1942), kept at SMNH.
L o c a l i t i e s. The type locality is an outcrop containing red-grey sandstones at the right bank of Imula River near Ģenduļi and Bienes hamlets, Latvia. Some specimens were collected from the Velna Ala locality at the left bank of Abava River.
H o r i z o n. The Pamušis Regional Substage (Ogre Formation).
D e s c r i p t i o n. Grossilepis spinosa is a small bothriolepidoid with estimated length of dorsal wall of trunk shield reaching about 6 cm. A poorly preserved La plate (Gross, 1942, Abb.9B) shows no significant information except the character of ornament bearing the concentrically set 5 to 6 ridges along the orbital margin and typical tubercles on the rest of the plate. The Nu plate is moderately wide with length/breadth index of 62 in holotype, with convex posterior margin bearing the sharp median process. The relatively broad anterior margin shows a shallow postpineal notch and broad orbital facets. The postero-lateral corners are slightly pronounced, but the lateral corners are well defined. The anterior division of the lateral margin is strikingly shorter than the posterior division. The obtected nuchal area is broad and possibly extents laterally far to the Pn plate. The external openings of the canal for the endolimphatic ducts are placed comparatively far anteriorly the obtected

nuchal area. The imperfect AMD plate lacking the posterior fourths is narrow with breadth/length index about 77. The anterior margin is convex with slightly defined antero-lateral corners. The lateral margin bears a well developed external postlevator process and a clearly defined lateral corner which is slightly pronounced. The left lateral margin as it is preserved shows the overlap areas both for the ADL and MxL plates; unfortunately the most posterior part of this margin is lost and it is difficult to estimate the posterior extent of the overlap area for the MxL plate. The levator fossa on the visceral surface is long and narrow. The postlevator crest is well pronounced. The proximal segment of the pectoral fin seems to be fairly slender. The relatively long and narrow Ml_2 plate, as well as Cd_1 show a strikingly long and pointed lateral spines. The ornament on the head-shield, trunk armour and Ml_2 plates consists of numerous closely and irregularly set tubercles.

R e m a r k s. This species was establish 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 plate, sutural connections between the AMD and MxL plates, as well as tuberculate ornamentation.

D i s c u s s i o n. *Grossilepis spinosa* resembles *Grossilepis tuberculata* by several features, but could be readily distinguished from it in its (1) other shape of the Nu plate and its posterior margin, (2) comparatively well defined lateral corner of the AMD plate, (3) character and shape of strongly developed long lateral spines of the proximal segment of pectoral fin. *Grossilepis spinosa* differs well from *G.brandi* Miles (1968) in its relatively narrower Nu plate and a proportions of the anterior and posterior divisions of the lateral margin of this plate.

Variability in bothriolepid antiarchs

There are many papers on modern evolutionary biology and paleontology dedicated to the variability of organisms. However, relatively few publications are devoted to variability of palaeozoic fishes, in particular placoderms. *Bothriolepis canadensis* Whiteaves from the lower Upper Devonian of Canada is in this respect the best known antiarch. The presence of large number of usually well-preserved individuals of all age groups in the collections of various museums, made possible the study of the morphology and growth of the head-shield and dorsal wall of the trunk-armour, as well as variability in the details of the sensory line pattern (Stensiö 1948; Graham-Smith 1978; Werdelin & Long 1986). Werdelin & Long noted the necessity of using statistical methods in the evaluation of features, and used regression analysis in their study of the allometric pattern of growth of the head-shield and dorsal wall of the trunk armour in *Bothriolepis canadensis*. As a result they managed to specify which bones change in proportions during the growth of the animal, and also in a later paper (Long & Werdelin 1986) to note differences in the growth pattern of some plates of newly described *Bothriolepis* species from Australia.

The species of *Bothriolepis* were previously distinguished mostly on basis of the proportions of the armour plates, with indication of unusual morphological features including the visceral surface of the head-shield, as well as ornamentation of the bones. Since Stensiö's work on the diagnoses of species, so called indices of bones, i.e. ratios of various measurements, have been used in comparing different species of antiarchs. For bothriolepidids and asterolepidids similar indices are of general use (Stensiö, 1948; Miles, 1968; Karatajūte-Talimaa, 1966; Lyarskaya, 1981). Werdelin and Long (1986) claimed that the use of indices in the diagnoses of species, as well as in comparing different species of antiarchs, without considering the age of the individuals, could lead to incorrect conclusions and the recognition of different growth stages as separate species. The study of age variability, including allometric growth, is therefore very important for phylogeny reconstructions of *Bothriolepis* and antiarchs in general, as well as for the recognition of species of *Bothriolepis*. Studies of uninterrupted variability limits are necessary to distinguish species from one another.

There are several other methods of evaluating phenotypical differences between populations and species, which have been used in palaeoichthyology (Vorobyeva & Minich 1968; Minich 1977). Usually they are based on the estimating of Mahalanobis distances, as well as some similar parameters, such as parameter CD proposed by Mayr (1971). Rarely, opportunities for more advanced methods such as correlation analysis (Krupina & Krupin 1983), are used. However, all the aforementioned methods, including the regression analysis, offer a typological approach according to which the variability of a mean value is similar to zero; consequently, the real extent of character variation is not taken into account. The mean square deviation of the variable from a mean value which, strictly speaking, could not be recognized, has usually been accepted as a parameter of variability.

Recently some papers have appeared, in which variability is determined as a "distance" or sum of differences between organisms (Cherepanov 1986). Cherepanov proposed a new method, consisting of an estimation of relative pair differences between organisms on basis of all their quantitative morphological features. For the population/species relative differences calculated after one variable are

$$d_{(m)} = \frac{2 \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} \left(\frac{|x_i - x_j| \times 100}{\max(x_i, x_j)} \right)}{n(n-1)}$$

where $d^{(m)}$: the mean difference after one variable m between all individuals, σ_i and σ_j: value of variable m in individuals i and j; n: number of individuals. The degree of mean difference between individuals after a set of variables, according to Cherepanov, is

$$d = \frac{1}{k} \sum_{j=1}^{k} \hat{d}_j$$

where $d_{(k)}$ - the mean differences between phenotypes depending on the sum of k variables. This parameter characterizes the mean distance between phenotypes in the population. It is close to the coefficient of variation; however, as far as distances are estimated comparing all individuals in pairs, instead of distances from the mean value, "Cherepanov's parameter" usually slightly exceeds the coefficient of variation.

The mean phenotypical differences between individuals in a population/species (d) and between different species (CD) are calculated according to Cherepanov in similar ways and are comparable in this sense. The method suggested by Cherepanov enables the creation of diagrams of the similarities/differences between phenotypes of compared species and populations.

Among the positive features of the suggested method should be mentioned the possibility to estimate the differences between species from relatively few specimens, minimum five (Cherepanov 1986). Cherepanov analysed the variability in several groups of recent animals, including fish, but such attempts relating to ancient organisms are unknown to us.

In this chapter I have summarized the results of using regression analisys, as well as the method suggested by Cherepanov, to study the variability and interrelationships of bothriolepids from the Main Devonian Field. 754 specimens of *Bothriolepis obrutschewi* Gross, *Bothriolepis cellulosa* (Pander), *Bothriolepis trautscholdi* Jaekel, *B.maxima* Gross, *B.evaldi* Lyarskaja, *B.curonica* Gross, *B.jani* Lukševičs, *B.ornata* Eichw., *B.ciecere* Lyarskaja and *Grossilepis tuberculata* (Gross) were investigated to assess the limits of the continuous variability and estimate "distances" between different species (Table 1 of Supplement). Among these species, *Bothriolepis obrutschewi*, *B.cellulosa* and *Grossilepis tuberculata* have also been measured using photographs of described specimens (Gross, 1942; Karatajūte-Talimaa, 1966). Most of the specimens are represented by disarticulated plates of the dermal armour, but some species include articulated head-shields.

The list of measurements follows Werdelin and Long (1986), but some additional measurements were taken (Table 2 of Supplement). Then indices of measurements, regression coefficients and correlation coefficients, as well as relative differences were calculated. For the analysis of variability 28 indices were selected, which, I suggest, most completely characterize the external morphological structure of fish armour (Table 2 of Supplement). The regression coefficients are calculated and tested as in Werdelin & Long (1986).

The calculation of correlation factors in *Bothriolepis ciecere* shows very close connections between several morphological features (Table 1) and confirms the suggestion of Werdelin & Long, that this pfenomenon could be explained by the peculiarities of growth of the rigid armour of the animal. Correlation analysis does not permit one to allocate more closely dependent and weakly dependent variables, and is thus useless for phylogenetic purposes in studying antiarchs.

Table 1. Correlation factors of the AMD features in *Bothriolepis ciecere* (n=21)

	L	W	Lt	Wa	Wp
L		0.979	0.982	0.939	0.955
W	0.979		0.960	0.968	0.981
Lt	0.982	0.960		0.932	0.935
Wa	0.939	0.968	0.932		0.955
Wp	0.955	0.981	0.935	0.955	

Of the seven *Bothriolepis* species for which the regression coefficients were calculated two (*Bothriolepis curonica, B.jani*) showed isometric growth patterns (Table 3 of Supplement). Other species showed different forms of allometric growth ranging from one

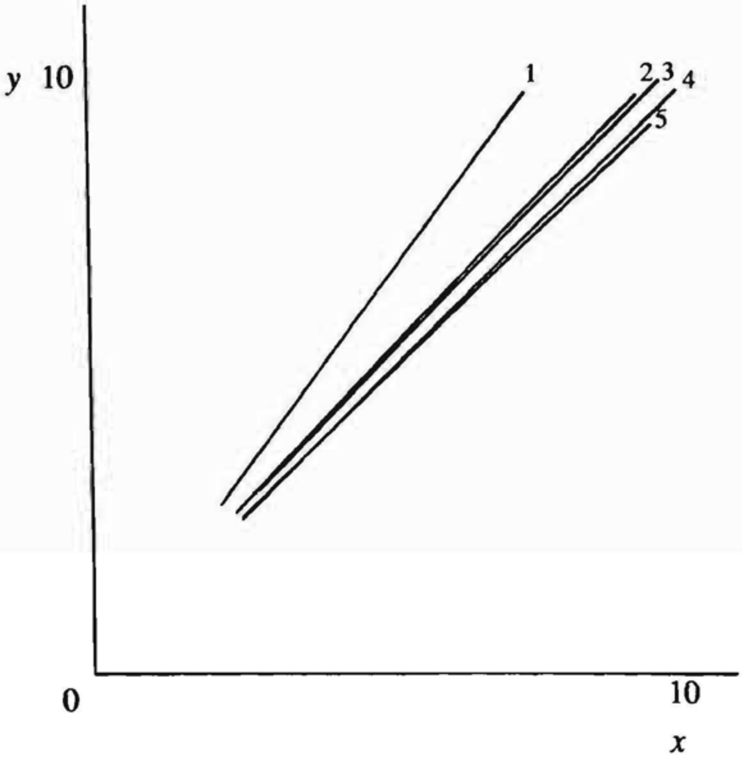
Table 2. The regression coefficients of selected variable pairs in several *Bothriolepis*

Species Variable pairs	tra	eva	max	cur	jan	orn	cie
LPrm/WrPrm	0.900	0.592	0.704	0.636	-	0.852	0.819
WrPrm/WoPrm	0.753	0.410	0.906	0.960	-	1.214	0.804
LNu/WNu	0.888	0.846	0.856	0.940	-	0.866	0.732
WOf/WHs	-	0.906	1.414	0.929	-	-	1.088
LHs/LPrm	-	1.525	0.989	1.923	-	-	0.491
LAMD/WAMD	0.998	1.306	0.983	-	0.828	1.022	1.032
LtAMD/LAMD	1.256	0.947	0.851	-	1.093	1.049	1.012
WaAMD/WpAMD	0.954	0.694	0.606	-	0.645	1.413	0.946
LPMD/WPMD	0.993	1.036	1.284	-	1.028	1.095	0.936
WaPMD/WPMD	1.229	0.816	0.834	-	1.006	0.885	0.874

The regression coefficients differing significantly from 1 are underlined. For abbreviations see Table 8.

variable pair (*B.ornata*: LPMD/WPMD) to seven pairs of variables (*B.evaldi*). Comparison of the regression coefficients of similar variable pairs in studied species of *Bothriolepis* showed that the regression slopes are usually almost parallel (Text-fig. 26) and differences between the regression coefficients are in most cases not significant (Table 2). This demonstrates that regression analysis is an important method for ascertaining the growth pattern. It is not so effective in the recognition of species, because it is characterized by an absence of sharp criteria to evaluate the degree of phylogenetic divergence; we cannot determine the "distances" between different species for a single feature, much less for a set of features.

The results of the analysis of variability in above mentioned species of Bothriolepididae obviously demonstrate the possibilities of Cherepanov's method. Comparison of the variability based on the sum of features in *Bothriolepis* from two Late Devonian localities (Ketleri and Pavāri) confirmed that the remains belong to the species *B.ciecere* (CD is in between the d_1 and d_2) (Table 3).



Text-fig.26. Regression slopes for the parameter L_{AMD}/W_{AMD} in various *Bothriolepis* species

1	*Bothriolepis evaldi*	$y = 1.306x + 0.096$
2	*B. ciecere*	$y = 1.032x + 0.068$
3	*B. ornata*	$y = 1.022x + 0.045$
4	*B. trautscholdi*	$y = 0.998x + 0.015$
5	*B. maxima*	$y = 0.983x + 0.113$

Table 3. Comparison of the variability of the AMD in *Bothriolepis ciecere* from the two localities

	d_{AMD}		CD_{AMD}
	Ketleri	Pavāri	Together
LAMD/WAMD	5.31	8.01	8.00
LtAMD/LAMD	6.68	7.08	6.98
LlAMD/LAMD	4.47	8.23	7.34
WAMD/WaAMD	10.61	11.26	10.90
WAMD/WpAMD	12.48	5.97	7.34

The most stable variables characterizing the general proportions of the head-shield (Table 4 of Supplement) are the relative width of the orbital fenestra (WOf/WHs; d=5.76 on average) and general proportions of the head-shield (WHs/LHs; d=6.76 on the average). The relative length of the praeorbital division of the head-shield which depends on the relative length of the praemedian plate is slightly more variable (LHs/LPrm; d=7.68 on average). In all four species of *Bothriolepis* in which the articulated head-shields are recorded the variability of the general proportions of the head-shield fall within moderately narrow limits (from 5.52 in *Bothriolepis curonica* to 8.51 in *B.evaldi*) (Table 4). As the parameters CD_{Hs} in all cases strongly exceed the parameters d_{Hs}, it is clearly seen that all four species differ well in the general proportions of the head-shield. The Prm plate is more strongly variable in its shape and proportions (Table 5 of Supplement; Table 5). *Bothriolepis cellulosa* has similar proportions of the Prm as *B.maxima* and *B.trautscholdi*. Other species differ clearly one from another.

Table 4. The parameters d_{Hs} and CD_{Hs} based on the sum of 3 pairs of variable in some *Bothriolepis* species

	Species	1	2	3	4
1	*B.ciecere*	<u>6.56</u>	16.26	13.29	15.00
2	*B.curonica*		<u>5.52</u>	24.98	10.12
3	*B.evaldi*			<u>8.51</u>	23.18
4	*B.cellulosa*				<u>5.96</u>

The parameters d_{Hs} are underlined.

Table 5. The parameters d_{Prm} and CD_{Prm} based on the sum of 2 pairs of variable in some *Bothriolepis* species

Species	1	2	3	4	5	6	7
1 *B.ciecere*	<u>6.31</u>	28.31	22.99	16.87	23.09	23.24	13.49
2 *B.curonica*		<u>8.92</u>	21.29	35.71	26.09	24.80	29.77
3 *B.maxima*			<u>7.23</u>	31.67	9.79	**10.08**	14.28
4 *B.evaldi*				<u>13.29</u>	31.80	32.04	24.42
5 *B.trautscholdi*					<u>8.77</u>	**10.09**	9.77
6 *B.cellulosa*						<u>12.10</u>	14.39
7 *B.obrutschewi*							<u>9.22</u>

The parameters d_{Prm} are underlined. The parameters CD_{Prm} which do not exceed d_{Prm} are shown in bold.

The nuchal plates are usually well preserved and known in almost all described species of *Bothriolepis*. The general proportion of the Nu plate (LNu/WNu) varies from 2.24 in *Bothriolepis ciecere* to 11.42 in *B.ornata* and reaches 6.65 on the average (Table 6 of Supplement). The relative length of the orbital margin (WNu/TNu) is slightly more variable; it is 7.47 on average, ranging from 5.16 in *B.jani* to 10.97 in *B.ornata*. The parameter d_{Nu} based on the sum of all three pairs of variables, is relatively stable and varies from 3.86 in *B.ciecere* to 12.21 in *B.ornata*; in most of the species this parameter reaches about 7 to 9. The Nu plate is very useful for the analysis of continuous variability and for recognition of species, as the parameters CD_{Nu} in almost all cases exceed well the parameters d_{Nu} of the compared pair of species (Table 6).

The paranuchal plates are also usually well preserved and known in almost all described species of *Bothriolepis*. The general proportions of the Pn plate (LPn/WPn) are strongly variable in each species, ranging from 6.80 in *Bothriolepis evaldi* to 16.09 in *B.cellulosa* and reaching 10.52 on average (Table 7 of Supplement). The relative width of the lateral division (WPn/WlPn) is one of the most stable variables. It averages 5.74, ranging from 2.12 in *B.ornata* to 9.76 in *B.trautscholdi*. The parameter d_{Pn}, based on the sum of the two pairs of variables, is moderately stable and varies from 6.30 in *B.ciecere* to 11.83 in *B.cellulosa*. Three groups of species of *Bothriolepis* could be separated on the base of the analysis of continuous variability in the Pn plate: *B.ciecere-B.ornata-B.curonica*, *B.maxima*, and *B.evaldi-B.trautscholdi-B.cellulosa-B.obrutschewi* (Table 7).

Table 6. The parameters d_{Nu} and CD_{Nu} based on the sum of 3 pairs of variables in some bothriolepids

Species	1	2	3	4	5	6	7	8	9	10
1cie	3.86	**10.14**	14.30	21.64	9.10	13.01	21.03	11.36	11.35	14.87
2 orn		12.21	17.75	17.58	13.20	12.68	17.13	**11.01**	12.63	13.17
3 jan			5.15	25.48	19.30	10.67	13.99	13.01	9.77	10.12
4 cur				7.25	18.47	20.58	18.57	17.67	20.37	18.91
5 max					8.31	18.59	25.79	15.99	16.67	19.66
6 eva						8.55	11.54	9.39	9.05	**7.71**
7 tra							7.16	13.23	13.61	10.35
8 cel								8.22	**8.53**	8.77
9 obr									8.75	**8.61**
10 tub										7.69

The parameters CD_{Nu} which do not exceed d_{Nu} are shown in bold. The parameters d_{Nu} are underlined. For abbreviations see Table 8.

Table 7. The parameters d_{Pn} and CD_{Pn} based on the sum of 2 pairs of variables in some bothriolepids

Species	1	2	3	4	5	6	7	8	9
1cie	6.30	**6.42**	**7.56**	7.38	11.06	10.54	11.84	**7.96**	15.61
2 orn		6.48	**7.05**	10.06	14.58	11.51	13.97	9.85	18.95
3 cur			8.21	10.98	14.45	11.35	13.55	9.88	10.73
4 max				6.52	9.02	12.58	11.93	9.19	12.41
5 eva					7.20	10.86	**9.46**	9.23	8.19
6 tra						10.79	**10.88**	**9.43**	12.94
7 cel							11.83	**10.10**	**11.30**
8 obr								8.36	12.79
9 tub									7.51

The parameters CD_{Pn} which do not exceed d_{Pn} are shown in bold. The parameters d_{Pn} are underlined. For abbreviations see Table 8.

The most stable variables of the AMD (Table 8 of Supplement) are the relative length of the anterior division of the plate (LlAMD/LAMD: d=6.62), the general proportions of a plate (LAMD/WAMD: d=6.93), and also such an important parameter as the position of the tergal angle (LtAMD/LAMD: d=6.76), which characterizes the passing of sensory line canals on the dorsal wall of the trunk armour maximum. The relative length of the posterior margin (WAMD/WpAMD: d=8.96) and the anterior margin (WAMD/WaAMD: d=12.13) are more strongly variable.

The parameter d_{AMD} based on the set of 5 variables varies from 5.04 in *Bothriolepis obrutschewi* to 10.25 in *B.jani* (Table 8). The variability of the shape and proportions of the AMD is greater in species with a high degree of allometry (*B.evaldi*).

Table 8. The parameters d_{AMD} and CD_{AMD} based on the sum of 5 pairs of variable in some *Bothriolepis* and *Grossilepis* species

Species	1	2	3	4	5	6	7	8	9	10
1cie	<u>8.14</u>	10.83	17.57	12.22	16.98	15.08	12.87	14.11	11.02	20.10
2 orn		<u>8.31</u>	16.98	10.66	13.00	14.73	12.82	12.97	10.13	20.12
3 jan			<u>10.25</u>	15.87	18.02	**9.86**	10.84	11.50	12.31	19.05
4 cur				<u>8.10</u>	15.87	12.86	12.10	12.46	11.03	18.54
5 max					<u>7.94</u>	15.42	15.05	15.40	12.26	25.35
6 eva						<u>9.04</u>	**8.73**	9.85	9.98	17.48
7 tra							<u>6.42</u>	**8.46**	6.98	15.56
8 cel								<u>8.74</u>	**8.73**	15.54
9 obr									<u>5.04</u>	17.74
10 tub										<u>10.81</u>

Abbreviations: obr - *Bothriolepis obrutschewi*; cel - *B.cellulosa*; tra - *B.trautscholdi*; eva - *B.evaldi*; max - *B.maxima*; cur - *B.curonica*; jan - *B.jani*; orn - *B.ornata*; cie - *B.ciecere*; tub - *Grossilepis tuberculata*. The parameters CD_{AMD} which do not exceed d_{AMD} are shown in bold. The parameters d_{AMD} are underlined.

The similar parameter CD_{AMD}, based on the sum of features for a pair of compared species, usually exceeds d_{AMD} (Table 8); in some cases there is no significant difference in the shape and proportions of the AMD between species. *Bothriolepis jani* resembles *B.evaldi* according to a set of variables, but differs in the length of the anterior margin. *B.evaldi* differs slightly from *B.trautscholdi* in the position of the tergal angle and the length of the anterior margin. *B.trautscholdi* only differs slightly from *B.cellulosa* in the length of the anterior and posterior margins. *B.cellulosa* differs from *B.obrutschewi* in the general proportions of the plate and in the length of its anterior division, but does not differ according to a set of variables.

Only two variables were used to analyse the variability of the PMD plate (Table 9 of Supplement, Table 9). The variable, which characterizes the general proportion of a plate (LPMD/WPMD) is more stable (d=7.58 on average) than the relative length of the anterior margin (WaPMD/WPMD: d=8.74). The proportions of the PMD in several *Bothriolepis* species do not differ as significantly as the proportions of the AMD. The parameters d_{PMD} are almost similar in pairs of species *Bothriolepis jani - B.evaldi, B.jani - B.cellulosa, B.jani - B.obrutschewi, B.maxima - B.trautscholdi, B.evaldi - B.cellulosa, B.evaldi - B.obrutschewi, B.trautscholdi - B.cellulosa, B.trautscholdi - B.obrutschewi, B.cellulosa - B.obrutschewi*. There are no differences in the proportions of the PMD between *B.jani* and other species of *Bothriolepis* except *B.ciecere, B.ornata* and *B.maxima*. Similarly, *B.evaldi* resembles *B.cellulosa* and *B.obrutschewi* in the same features, and *B.cellulosa* resembles *B.obrutschewi* in this respect. Consequently, the analysed features (especially the relative length of the anterior margin of the PMD) have more limited significance in the recognition of *Bothriolepis* species than the feature of the AMD plate. Nevertheless, the parameter d_{PMD} differs dramatically in all the species of *Bothriolepis* comparing with that of *Grossilepis*. *B.ciecere* and *B.ornata* also differ in the same parameter from all the other species of *Bothriolepis*.

Two variables characterizing the general proportion of a dorsal lamina of the ADL plate (LADL/WADL) and a relative length of its posterior margin were used to analyse the variability of this plate in five species of *Bothriolepis* (Table 10 of Supplement, Table 10). Both features are strongly variable, the first one is slightly more stable (d=9.69 on the average) than the second one (d=10.30). The proportions of the ADL not differ in several *Bothriolepis* so significantly as the proportions of the AMD. The parameters d_{ADL} are almost similar in pairs of species *Bothriolepis maxima - B.evaldi, B.maxima - B.trautscholdi* and *B.trautscholdi - B.obrutschewi*. *B.ciecere* differs well from all the other species of *Bothriolepis* in the parameter d_{ADL}.

Table 9. The parameters d_{PMD} and CD_{PMD} based on the sum of 2 pairs of variable in some *Bothriolepis* and *Grossilepis* species

Species	1	2	3	4	5	6	7	8	9
1 cie	6.49	15.15	17.17	19.29	16.73	16.07	17.60	13.91	23.78
2 orn		8.10	13.25	17.10	11.99	14.07	12.32	9.74	16.53
3 jan			9.32	12.08	**8.75**	10.18	**9.89**	**8.33**	14.44
4 max				6.88	11.86	**8.97**	11.55	10.96	22.97
5 eva					9.74	10.06	**9.90**	**8.04**	16.28
6 tra						9.32	**10.50**	**8.76**	19.58
7 cel							10.69	**9.22**	16.95
8 obr								6.07	16.90
9 tub									6.86

The parameters CD_{PMD} which do not exceed d_{PMD} are shown in bold. The parameters d_{PMD} are underlined. For abbreviations see Table 8.

Table 10. The parameters d_{ADL} and CD_{ADL} based on the sum of 2 pairs of variable in some *Bothriolepis* species

Species	1	2	3	4	5
1 *B.ciecere*	9.26	22.50	26.16	21.31	18.54
2 *B.maxima*		11.49	**9.86**	**10.72**	13.21
3 *B.evaldi*			8.86	10.46	13.03
4 *B.trautscholdi*				10.13	**9.95**
5 *B.obrutschewi*					10.24

The parameters CD_{ADL} which do not exceed d_{ADL} are shown in bold. The parameters d_{ADL} are underlined.

Two variables characterizing the general proportion of a dorsal lamina of the MxL plate (LMxL/WMxL) and a relative length of its anterior margin (WMxL/WaMxL) were used to analyse the variability of this plate in eight species of *Bothriolepis* and the relative height of the lateral lamina (LMxL/HMxL) was analised in four species (Table 11 of

Supplement, Tables 11, 12). The general proportion of a dorsal lamina of the MxL plate is comparatively stable ranging from 3.47 in *Bothriolepis maxima* to 6.90 in *B.obrutschewi* and reaching only 5.04 on the average. The relative length of the anterior margin is strongly variable (10.55 on average). The relative height of the lateral lamina varies from 4.77 in *B.curonica* to 10.34 in *B.jani*, reaching 8.30 on the average. The proportions of the MxL differ in several *Bothriolepis* more significantly than the proportions of the ADL. The parameters d_{MxL} are similar in pairs of species *Bothriolepis ciecere* - *B.curonica*, *B.ornata* - *B.curonica*, *B.jani* - *B.trautscholdi* and *B.evaldi* - *B.obrutschewi*.

Table 11. The parameters d_{MxL} and CD_{MxL} based on the sum of 2 pairs of variable in some *Bothriolepis* species

Species	1	2	3	4	5	6	7	8
1 cie	6.37	**8.24**	**8.44**	**6.80**	12.92	13.07	8.32	13.45
2 orn		9.52	10.79	**9.40**	15.81	15.92	12.00	16.97
3 jan			6.19	7.47	**8.49**	8.92	**6.16**	8.91
4 cur				6.96	11.41	11.58	7.37	11.37
5 max					10.50	**9.40**	**8.72**	**9.13**
6 eva						8.49	8.80	**8.12**
7 tra							6.32	8.30
8 obr								8.01

The parameters CD_{MxL} which do not exceed d_{MxL} are shown in bold. The parameters d_{MxL} are underlined. For abbreviations see Table 8.

Table 12. The parameters d_{MxL} and CD_{MxL} based on the sum of 3 pairs of variable in some *Bothriolepis* species

Species	1	2	3	4
1 *B.ciecere*	7.24	14.70	6.88	13.31
2 *B.jani*		7.57	14.02	11.68
3 *B.curonica*			6.23	11.62
4 *B.obrutschewi*				8.37

The parameters d_{MxL} are underlined.

Table 13. The parameters d_{AVL} and CD_{AVL} based on the 1 pair of variables in some *Bothriolepis* species

Species	1	2	3	4	5
1 *B.ciecere*	12.79	**11.57**	25.45	22.86	23.58
2 *B.curonica*		10.98	22.89	20.20	20.98
3 *B.maxima*			6.73	**8.46**	**6.08**
4 *B.evaldi*				10.19	**8.19**
5 *B.trautscholdi*					8.51

The parameters CD_{AVL} which do not exceed d_{AVL} are shown in bold. The parameters d_{AVL} are underlined.

Only one variable characterizing the general proportion of a ventral lamina of the AVL plate (LAVL/WAVL) was used to analyse the variability of this plate in five species of *Bothriolepis* (Table 12 of Supplement, Table 13). This parameter is comparatively strongly variable ranging from 6.73 in *Bothriolepis maxima* to 12.79 in *B.ciecere* and reaching 9.84 on the average. The proportions of the AVL not differ in several *Bothriolepis* significantly.

The general proportion of the ventral lamina of the PVL plate (LPVL/WPVL) is moderately stable variable ranging from 6.88 in *Bothriolepis curonica* to 10.36 in *B.obrutschewi*, reaching 8.48 on the average (Table 12 of Supplement, Table 14). The proportions of the AVL not differ in several *Bothriolepis* species significantly, only *B.maxima* differs well from all the other species in its very broad PVL.

Table 14. The parameters d_{PVL} and CD_{PVL} based on the 1 pair of variables in some *Bothriolepis* species

Species	1	2	3	4	5	6
1 cie	7.45	16.16	8.89	11.76	9.68	**9.37**
2 cur		6.88	21.68	**8.43**	10.44	12.10
3 max			8.41	16.28	13.88	13.21
4 eva				8.73	**8.27**	**9.65**
5 tra					9.07	**8.83**
6 obr						10.36

The parameters CD_{PVL} which do not exceed d_{PVL} are shown in bold. The parameters d_{PVL} are underlined. For abbreviations see Table 8.

The variability of the pectoral fin bones is shown in Table 13 of Supplement and Tables 15-17. The proportions of the central dorsal and central ventral plates 1 are relatively stable variables, but the proportions of the Ml_2 plate are more strongly variable. In most cases there are no significant differences between the species except *Bothriolepis curonica* differs well from all the other *Bothriolepis* in its slender Ml_2 plate.

Table 15. The parameters d_{Cd} and CD_{Cd} based on the 1 pair of variable in some *Bothriolepis* species

Species	1	2	3	4
1 *B.ciecere*	5.73	**5.99**	6.31	9.41
2 *B.evaldi*		7.53	**7.03**	10.49
3 *B.obrutschewi*			5.12	**7.57**
4 *B.cellulosa*				9.23

The parameters CD_{Cd} which do not exceed d_{Cd} are shown in bold. The parameters d_{Cd} are underlined.

Table 16. The parameters d_{Cv} and CD_{Cv} based on the 1 pair of variable in some *Bothriolepis* species

Species	1	2	3	4	5
1 *B.ciecere*	4.58	**6.05**	9.76	9.47	**6.21**
2 *B.curonica*		7.01	12.87	11.09	8.26
3 *B.maxima*			7.89	**7.80**	9.12
4 *B.trautscholdi*				9.32	9.40
5 *B.obrutschewi*					7.88

The parameters CD_{Cv} which do not exceed d_{Cv} are shown in bold. The parameters d_{Cv} are underlined.

Table 17. The parameters d_{Ml} and CD_{Ml} based on the 1 pair of variables in some *Bothriolepis* species

Species	1	2	3	4	5
1 *B.ciecere*	7.12	**8.78**	28.87	**10.92**	**9.43**
2 *B.jani*		12.43	28.82	**11.65**	**11.22**
3 *B.curonica*			13.97	32.91	22.99
4 *B.evaldi*				13.82	15.00
5 *B.maxima*					9.44

The parameters CD_{Ml} which do not exceed d_{Ml} are shown in bold. The parameters d_{Ml} are underlined.

The analysis of the importance of several indices for the recognition of species shows nine pairs of variable with limited significance: e.g. only in 32 per cent of all cases species of genus *Bothriolepis* differ in the relative length of the anterior margin of the MxL plate (WMxL/WaMxL); other eight indices shows the differences between the species in slightly more often cases (WHs/LHs: 33%; LPn/WPn: 36%; WaPMD/WPMD: 39%; LlAMD/LAMD: 42%; LLa/WLa, LCd_1/WCd_1, LMl_2/WMl_2: 50% of cases). On the other hand, ten of indices are very important to be used in recognition of species showing the significant difference between species in more than 70 per cent of cases (LPrm/WrPrm, WAMD/WaAMD and LtAMD/LAMD: 71-72%; LADL/WADL, LMxL/WMxL, WNu/TNu and LHs/LPrm: 80-83%; WrPrm/WoPrm, LMxL/HMxL and WOf/WHs: more than 85%).

The analysis of distribution of parameters CD_{AMD} and d_{AMD} were used to create a tentative diagram showing a hypothesis of bothriolepid interrelationships, based on the variability of the shape and proportions of the AMD plate (Text-fig. 27). Cherepanov's method allows to find the quantitative differences between species and it is possible to create a diagram based on the quantitative features rather than on the alternative features. *Grossilepis tuberculata* differs well from all the other bothriolepids, most strikingly in a very broad posterior margin of the AMD plate. The representatives of *Bothriolepis* could be subdivided into three groups: *B.obrutschewi; B.trautscholdi - B.evaldi - B.jani - B.maxima,* which possess a relatively broad AMD plate with the anterior division of the lateral margin only slightly longer than the posterior division; *B.cellulosa - B.curonica - B.ornata - B.ciecere* characterize by a relatively narrower AMD plate with the anterior division of the

Table 18. The 'Cherepanov parameters' d, based on the sum of all quantitative feature, in several bothriolepid species

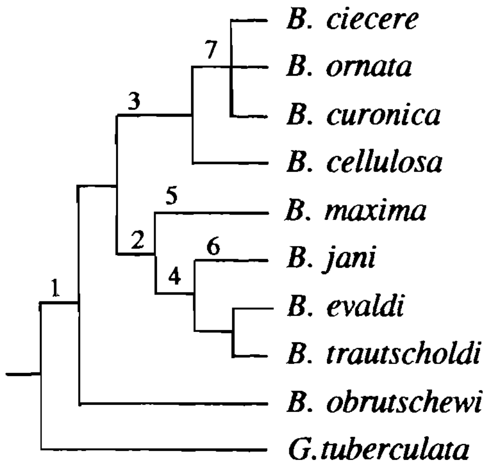
	number of variables k	d_k
B.ciecere	28	6.82
B.ornata	15	8.80
B.jani	14	8.60
B.curonica	24	7.92
B.maxima	22	8.11
B.evaldi	26	9.16
B.trautscholdi	23	8.20
B.cellulosa	19	9.16
B.obrutschewi	24	7.35
G.tuberculata	12	8.82

Table 19. The parameters d_k and CD_k based on the sum of all pairs of variables k in some bothriolepid species

Species	1	2	3	4	5	6	7	8	9	10
1cie	6.82	9.88	15.65	14.57	15.02	13.99	14.40	14.43	11.71	18.66
		15	14	23	22	27	24	19	23	12
2 orn		8.80	9.80	11.12	13.30	13.43	13.21	12.32	11.50	17.59
			19	13	15	15	15	13	15	12
3 jan			8.60	17.98	15.76	9.72	10.74	11.63	10.97	15.45
				11	12	12	12	10	13	10
4 cur				7.92	15.00	18.66	14.80	14.61	14.63	16.99
					19	21	19	16	18	11
5 max					8.11	14.61	13.22	13.58	12.37	21.38
						21	22	15	21	12
6 eva						9.16	11.84	14.16	10.91	13.29
							22	19	21	12
7 tra							8.20	10.23	9.32	14.49
								15	21	12
8 cel								9.16	9.55	13.38
									16	12
9 obr									7.35	14.49
										12
10 tub										8.82

The parameters d_{Nu} are underlined. The parameters CD_k are shown above and number of pairs of variable k below. For abbreviations see Table 8.

lateral margin well longer than the posterior division. *B.maxima* is placed aside within the second group due to the extremely narrow anterior margin of the AMD; other species of this group have a broad anterior margin, which is of moderate breadth in *B.trautscholdi* and *B.evaldi* and very broad in *B.jani*. *B.curonica, B.ornata* and *B.ciecere* compose a well defined subgroup within the third group of species; they differ from B.cellulosa in a narrow both anterior and posterior margins of the AMD.



Text-fig.27. Diagram showing hypothesis on phylogenetical relationships of bothriolepids from the Main Devonian Field, based on the change of shape and proportions of the AMD

1 AMD broadest across lateral angles, posterior margin short

2 broad AMD; anterior division of lateral margin only slightly longer that posterior division

3 narrow AMD; anterior division of lateral margin well longer that posterior division

4 broad anterior margin

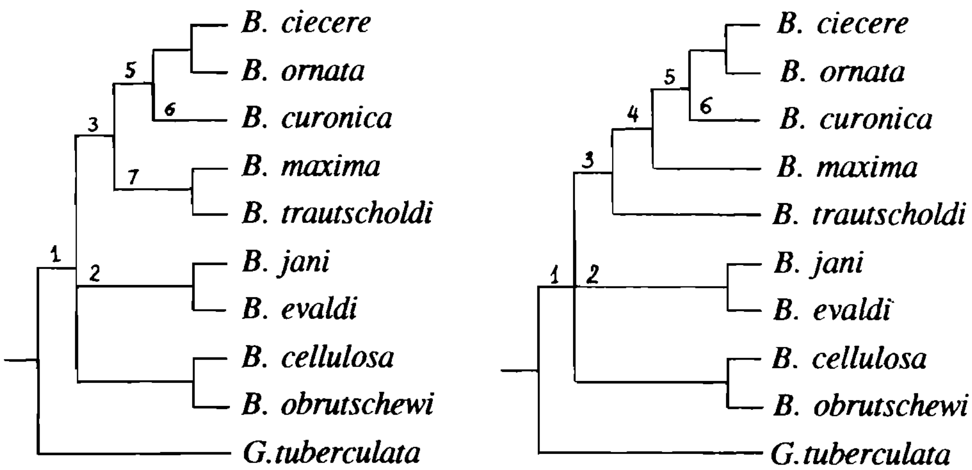
5 narrow anterior margin

6 very broad anterior margin

7 narrow anterior and posterior margins

The limits of "the parameter of Cherepanov" for several species of recent fishes varies from 4.50 to 12.26 (Cherepanov, 1986). The parameter of variability is more or less stable in studied species of *Bothriolepis* and varies from d_{28} = 6.82 in *Bothriolepis ciecere* to d_{26} = 9.16 in *B.evaldi* and d_{19} = 9.16 in *B.cellulosa* (Table 18).

The parameters CD_k based on the sum of all quantitative features (Table 19) in all cases exceeds the parameters d_k showing all the investigated taxa differ one from another. The analysis of distribution of parameters CD_k and d_k is used to create a diagram showing a hypothesis of bothriolepid interrelationships, based on the variability of all their quantitative features (Text-fig. 28).



Text-fig.28. Diagrams showing two hypotheses on phylogenetical relations of bothriolepids from the Main Devonian Field

1 AMD broadest across lateral angles, posterior margin short, MxL broadest across dorsal angle

2 AMD with broad anterior margin

3 AMD with short anterior margin and well developed pronounced postlevator processes

4 pentagonal praeorbital recess

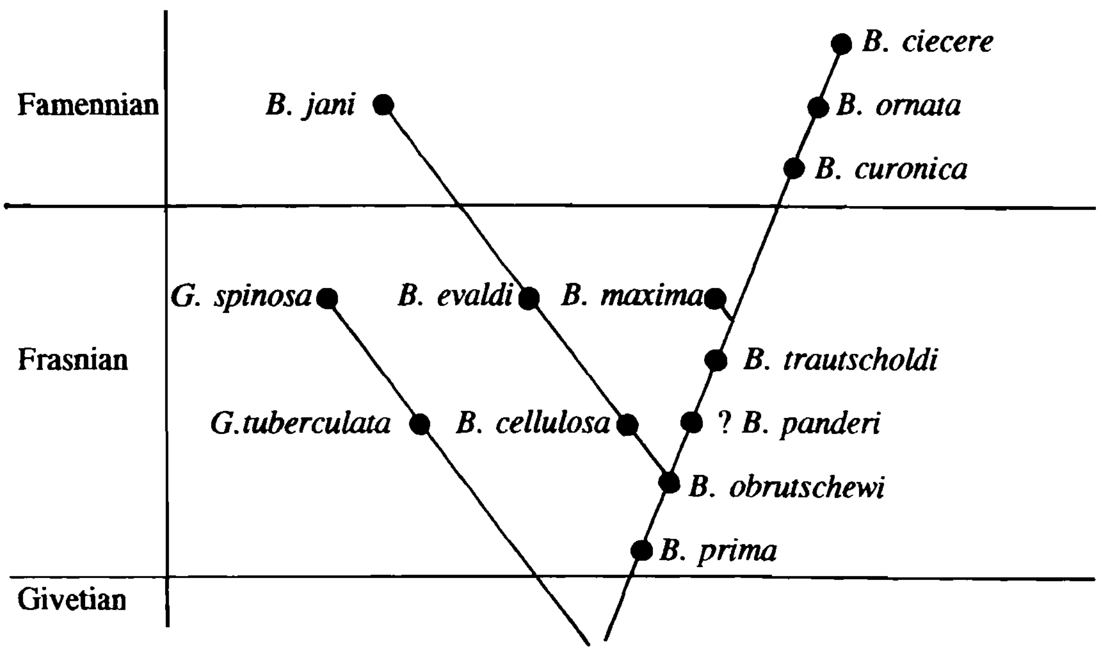
5 narrow AMD

6 slender pectoral fin, Nu with very short orbital margin, elongated PVL

7 very broad AMD and PMD

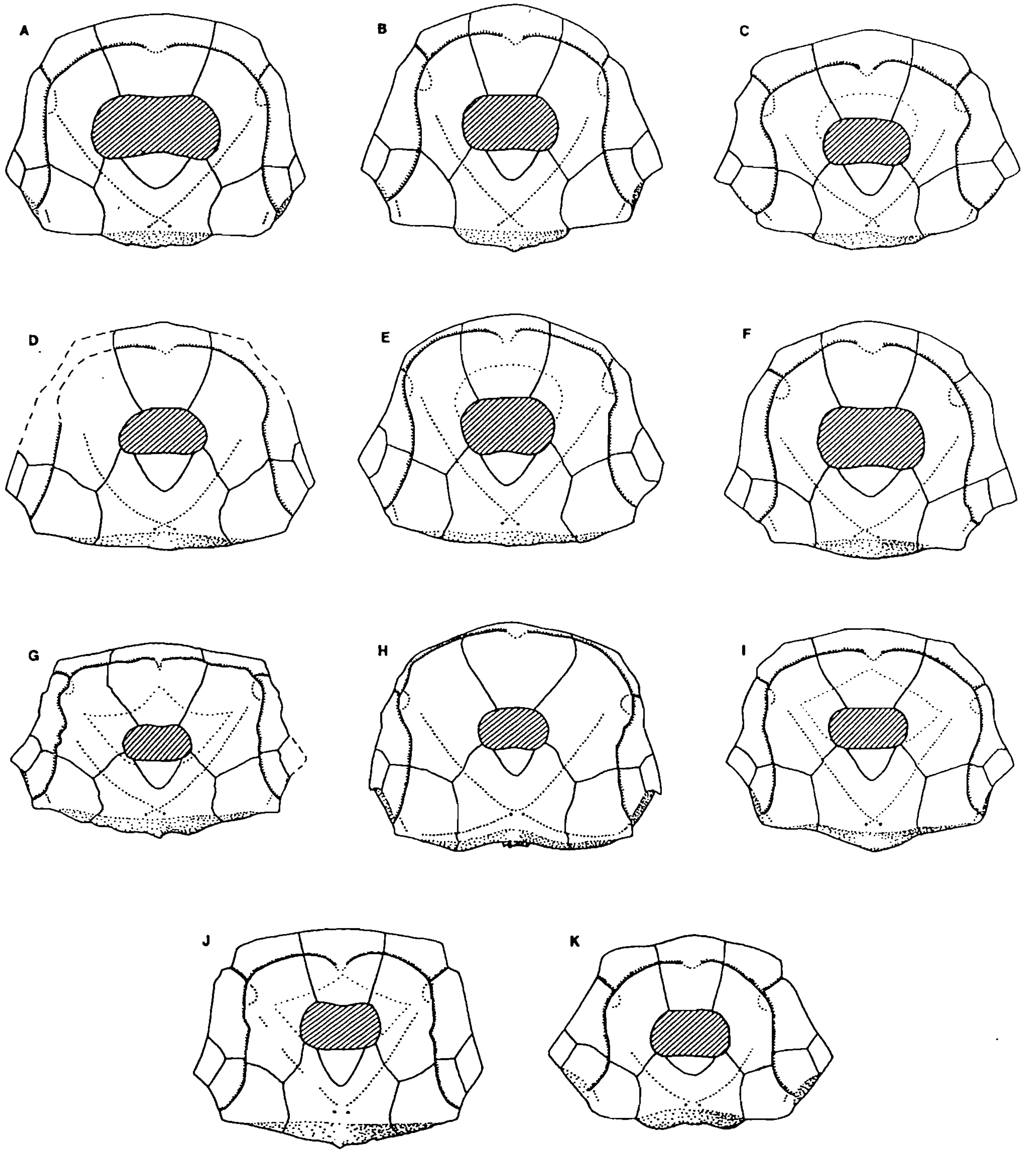
The analisys of data matrix shows that *Grossilepis tuberculata* significantly differs from all representatives of genus *Bothriolepis*, first of all in the shape and proportions of the AMD, MxL and Nu plates. *Bothriolepis cellulosa* is closely related to *B.obrutschewi*. *B.jani* resembles *B.evaldi* by the set of features, what probably could be explained by their small size and high degree of allometric pattern of growth. Both differs well from the other species in their relatively broad anterior margin of the AMD plate. The third large group of species is sharing the short anterior margin of the AMD plate with well defined pronounced postlevator processes. It is possible to create two different diagrams depending on the selected features. Both are similar in that *B.ciecere* and *B.ornata* are probably morphologically closely related species, and *Bothriolepis curonica* differs from them in its slender pectoral fin, a short orbital margin of the Nu plate and elongated PVL. These two diagrams differ in the position of *B.maxima* and *B.trautscholdi*. Both are characterised by very broad AMD and PMD plates, differing from *B.curonica, B.ornata* and *B.ciecere*, which have narrow AMD and PMD. The head-shield of *B.trautscholdi* have the praeorbital recess of simple type, like *B.cellulosa*; *B.maxima* differs in its trifid-type praeorbital recess sharing this feature with *B.ornata* and *B.ciecere* (the shape of prh is unknown in *B.curonica*) (text-fig. 30). The latter diagram seems therefore to be more evident.

Comparison of two hypotheses based on the features of the AMD plate and all the morphological feature shows they are more or less congruent, but using all the quantitative features provides possibility to create a hypothesis which is more reliable and coincides with the stratigraphical distribution or age of bothriolepid species (Text-fig.29).



Text-fig.29. Hypothesis on phylogeny of bothriolepids from the Main Devonian Field

The comparison of the diagrams proposed here with the cladogram for various species of *Bothriolepis* (Young, 1988) shows that Cherepanov's method is another good tool which could provide more information adding the cladistic analysis.



Text-fig. 31. Comparison of the head-shields and praeorbital recess shape in several species of *Bothriolepis* and *Grossilepis*. A, *Bothriolepis prima* (from Karatajūte-Talimaa, 1966). B, *B.obrutschewi* (from Karatajūte-Talimaa, 1966). C, *B.cellulosa* (from Gross, 1941). D, *B.panderi*, restoration based on lectotype MM 1/96. E, *B.trautscholdi*, restoration based on specimen PIN 330/117. F, *B.evaldi*, restoration based on specimen LDM 280/1. G, *B.maxima*, restoration based on specimen LDM 99/1. H, *B.curonica*, restoration based on specimen LDM 89/1. I, *B.ornata*, restoration based on specimen LDM 100/32. J, *B.ciecere*, restoration based on specimens LDM 43/337, 81/101, LGI 5/2034A. K, *Grossilepis tuberculata* (from Gross, 1941). Not to scale.

Distribution and biostratigraphy

Bothriolepidoids are among the most widely distributed and frequently found vertebrates from the Main Devonian Field. The genus *Bothriolepis* is characterized by high diversity and comparatively quick evolution. It is therefore regarded as very 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. A short essay on the geographical distribution of bothriolepidoids, in stratigraphic sequence, is provided below.

The earliest reported occurence of *Bothriolepis* is in China, where Pan (1981) has identified three named *Bothriolepis* zones of Middle Devonian age, and in the Aztec Siltstone of Antarctica (Young, 1988). The oldest remains of *Bothriolepis* in the Main Devonian Field, of probably 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 and hence the Givetian/Frasnian boundary on the East European Platform have not been determined as yet. The lower boundary of the Upper Devonian and Frasnian Stage is the base of the Lower *P.asymmetricus* conodont Zone defined by the first occurence of *Ancyrodella rotundiloba*. According to the traditional point of view the base of the Frasnian in the Baltic sequence corresponds to the base of the Gauja Regional Stage (Rzhonsnitskaya, Kulikova, 1990). Mark-Kurik (1993) claimed that the Abava, Gauja and Amata Formations belong to the Givetian and proposed placing the lower boundary of the Frasnian higher, at the base of the Pļaviņas Regional Substage, i.e. at the base of the Snetnaya Gora Beds (see also Ivanov, 1993).

Recently a new study of the conodonts from the stratotypes of the Timan Formation and Ust'e Yarega Formation was conducted in South Timan (Kuzmin, 1995). The analysis of the distribution of conodonts showed that the base of the Lower *P.asymmetricus* conodont Zone and hence the lower boundary of the Frasnian should be placed within the Timan Formation. The Ust'e Yarega Formation corresponds to part of the Pļaviņas Regional Substage of the Main Devonian Field. The upper part of the Timan Formation contains the vertebrate assemblages similar to that of the Pļaviņas Formation. The lower boundary of the Upper Devonian of the Main Devonian Field should therefore be placed at the base of Pļaviņas Regional Substage, or at the base of the Amata Regional Substage or within the latter.

All studied *Bothriolepis* material from the Main Devonian Field comes mostly from the Upper Devonian deposits. There are 16 bothriolepidid taxa known now from the Main Devonian Field: *Bothriolepis prima*, *B.obrutschewi*, *B.cellulosa*, *B.panderi*, *B.trautscholdi*, *B.maxima, B.evaldi, B.curonica, Bothriolepis heckeri* sp.nov., *B.ornata, B.jani, Bothriolepis* sp.indet.1, *Bothriolepis* sp.indet.2, *B.ciecere, Grossilepis tuberculata, G.spinosa.*

Two broad assemblages characterized by faunal elements associated with the various species of *Bothriolepis* are recognized in the Main Devonian Field (Table 14 of Supplement). 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.

A m a t a Regional Substage contains the Amata Formation in Latvia, Upper Šventoji Subformation in Lithuania, Staritsa and Podsnetnaya Gora Beds in Russia, which are represented mostly by sandstones and clays, usually without invertebrates. *Bothriolepis prima* is represented by a large number of individuals and characterized by a relatively wide distribution, occuring in the middle part of the Amata Formation (Pastamuiža locality at Daugava River), Upper Šventoji Formation (outcrops at Pelyša River) and Staritsa Beds in Leningrad region (Yam-Tessovo locality at Oredezh River). The remains of *B.prima* were found at Pelyša River in bluish-grey siltstones together with bones of *Asterolepis ornata* Rohon, *Psammolepis* sp., *Plourdosteus livonicus* (Eastman), sarcopterygian scales and teeth and phyllopod shells. Abundant plates of *B.prima* occur in the red-brown and yellow-grey sandstones in Eastern Latvia (Pastamuiža at Daugava River) and Leningrad region. Beside *B.prima* the remains of *A.radiata*, *Glyptolepis baltica* Gross, *Laccognathus panderi* Gross, *Holoptychius* sp., an undetermined osteolepidid, *Panderichthys* cf.*rhombolepis* (Gross), *Eusthenopteron saevesoederberghi* Jarvik were reported from the well described (Karatajūte-Talimaa, 1966; Vorobyeva & Lyarskaya, 1968) and sampled Pastamuiža locality.

Bothriolepis obrutschewi Gross is a more widely distributed species than *B.prima*. The remains of *B.obrutschewi* were found in the upper part of the Amata Formation in the Pastamuiža locality, in two outcrops along Pelyša River, borehole Paroveja, 49.65-49.75 m deep (Upper Šventoji Formation), in the outcrop at the right bank of Velikaya River near Piskovichi hamlet some km N from Pskov city (Podsnetnaya Gora Beds) and in the Yam-Tesovo locality. This species together with *Asterolepis radiata*, *Psammosteus praecursor* and some sarcopterygians were recorded from the Middle Timan, the localities at Pechorskaya Pizhma River (the Ust'e Chirka Formation) and with slight doubt from the North Timan (the Kumushka Formation).

A rich vertebrate assemblage is recognized from the white sandstones of the Pastamuiža locality. Abundant disarticulated plates of the trunk armour and often articulated head-shields and pectoral fins of *B.obrutschewi*, more rare plates of *A.radiata*, branchial plates and fragments of shields of the heterostracans *Psammolepis undulata, Psammosteus livonicus, P.praecursor*, remains of the acanthodian *Archaeacanthus quadrisulcatus*, the sarcopterygians *Glyptolepis baltica*, *Laccognathus panderi*, *Holoptychius* sp., *Panderichthys* cf.*rhombolepis*, and an undetermined dipterid were collected there. In Lithuania the remains of *B.obrutschewi* were reported from the light yellow-grey, greenish-grey sandstones exposed at the right bank of Pelyša River (tributary of Šventoji River). Three well preserved parts of articulated trunk armour of this species were found in red-brown clays from the borehole Paroveja (Karatajūte-Talimaa, 1966).

P ļ a v i ņ a s Regional Substage is subdivided into Snetnaya Gora, Pskov and Chudovo Beds. The deposits of this substage consist mainly of limestones, marls, dolomites and dolomite marls with abundant and often diverse remains of marine invertebrates. Three species of bothriolepidoids: *Bothriolepis cellulosa* (Pander), *B.panderi* Lahusen and *Grossilepis tuberculata* (Gross) are represented in the vertebrate assemblages from the Pļaviņas Regional Substage. The Snetnaya Gora Beds deposits ("Cellulosa-Mergel" of Gross (1942) 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: the heterostracans *Psammosteus maeandrinus* Ag., *P.asper* Obr., *Karelosteus weberi* Obr., the placoderms *Ctenurella pskovensis* (Obr.), "*Ptyctodus*" sp., *Rhynchodus* sp., *Plourdosteus mironovi* (Obr.), *Asterolepis radiata* Rohon, *Bothriolepis cellulosa*, *B.panderi*, *Grossilepis tuberculata*, the acanthodian *Haplacanthus perseensis* Gross, chondrichthyans, the sarcopterygians *Holoptychius* sp., *Glyptolepis* sp., *Laccognathus* sp., *Latvius grewingki* Gross, *Eusthenopteron saevesoederberghi* Jarvik, *Strunius rolandi* (Gross), *Rhinodipterus secans* Gross, *Griphognathus minutidens* Gross and the palaeoniscid *Moythomasia perforata* (Gross) (Ivanov, 1990, with some taxa added by author). This broad assemblage is represented by three variants depending on the facial conditions: so-called Jiera, Snetnaya Gora s.stricto and Syas' assemblages. The first variant of the assemblage occurs in Western Latvia and Lithuania, where sandstones, clays and dolomites dominate the sequence. Psammosteid *P.maeandrinus*, antiarchs *Asterolepis radiata*, *Bothriolepis cellulosa*, *Grossilepis tuberculata*, porolepiforms and osteolepiforms dominate the assemblage.

The second variant of the broad assemblage was first described by Gross (1933, 1941, 1942); it is more widely distributed than the others and 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, yielding abundant remains of the antiarchs *Asterolepis radiata*, *Bothriolepis cellulosa*, and *Grossilepis tuberculata*, as well as the sarcopterygians *Latvius grewingki*, *Strunius rolandi*, more rare *Eusthenopteron saevesoederberghi*, *Glyptolepis* and *Laccognathus*, abundant dipnoans *Rhinodipterus secans* and rare *Griphognathus minutidens*, placoderms *Ctenurella pskovensis*, more rare "*Ptyctodus*", *Rhynchodus*, *Rhamphodopsis*, *Plourdosteus mironovi* and the palaeoniscid

Moythomasia perforata. The heterostracan *Psammosteus maeandrinus* Ag., *Asterolepis radiata*, acanthodians and chondrichthyans are very rare.

The third, Syas' variant of the assemblage is distributed in north eastern part of the Main Devonian Field, where terrigenous deposits dominate the sequence (Sorokin, 1978). The psammosteids *Psammosteus maeandrinus*, sometimes *P.asper* and *Karelosteus weberi*, the sarcopterygians *Holoptychius*, *Glyptolepis*, *Eusthenopteron*, and the placoderms *Asterolepis radiata*, *Bothriolepis panderi* and *Plourdosteus mironovi*, are dominant there. The dipnoan *Rhinodipterus* and palaeoniscid *Moythomasia* are rare, and acanthodians and ptyctodonts are very rare. *Grossilepis tuberculata* is probably stratigraphically the most widely distributed species among the Pļaviņas Regional Substage bothriolepids; it occurs from the Snetnaya Gora to the Chudovo Beds (Sorokin, 1978). The remains of this species were found in the Snetnaya Gora Beds 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 not far from Kārļi and along Mazā Jugla and Lielā Jugla Rivers, outcrops at Venta River near Kuldīga and at Riežupe River; see also 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). The remains of *G.tuberculata* are very rare in the Pskov Beds and until now reported only from Eastern Latvia (Sorokin, 1978). *Bothriolepis cellulosa* is a characteristic species for the Snetnaya Gora and Pskov Beds and is recorded mostly from the same localities as *Grossilepis tuberculata*. Additionally, *B.cellulosa* was 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), outcrop of dolomites and dolomite marls at Riežupe River near Kaļķi hamlet, approximately 6 km N from Kuldīga town, as well as from Ukhta River, the deposits of the Lower Ust'e Yarega Formation of the South Timan, the Ust'e Srednyaya Beds and the Srednyaya Beds of the Ust'e Yarega Formation of the Middle Timan (Pizhma River), as well as in Belarus. The remains of *Bothriolepis panderi* come from the outcrop of the Snetnaya Gora Beds at the right bank of Syas' River not far from Montsevo village.

D u b n i k Regional Substage 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. Sometimes the deposits of the Dubnik Regional Substage in Baltic region 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 sandstones, siltstones, clays and marls. Siltstones, silty marls and clays exposured along the Syas' River, contain a rich concentrations of vertebrate remains, lingulids, carbonized plants and ichnofossils. The reachest locality is located at the right bank of Syas' River near Stolbovo village. Several authors published descriptions of fishes and agnathans from this locality; the vertebrate assemblage from the site was defined by Obruchev & Mark-Kurik (1965), Vorobyeva (1977) etc. Up to now at least 14 taxa are described from this locality: the psammosteid *Psammosteus megalopteryx* (Trautschold), the placoderms *Rhynchodus* sp., *Holonema radiatum* Obr., *Gyroplacosteus panderi* Obr., *Plourdosteus trautscholdi* (Eastm.), *Eastmanosteus egloni* (O.Obr.), *Asterolepis syasiensis* Lyarskaya and *Bothriolepis trautscholdi* Jaekel, the acanthodian *Persacanthus* sp., and the sarcopterygians *Holoptychius* cf.*nobilissimus* Ag., *Jarvikina wenjukovi* (Rohon), *Parapanderichthys stolbovi* (Vorob.), *"Dipterus" verneuili* Pander and *Rhinodipterus stolbovi* Krupina. The vertebrate assemblage containing *Psammosteus megalopteryx* was recognized in the Ust'e Bezmoshitsa Formation of North Timan.

D a u g a v a Regional Substage 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 and Lithuania and with layers of multicoloured sandstones, siltstones and clays in its eastern part. The vertebrate remains are very rare and usually poorly preserved in western part of the Main Devonian Field. Scarce remains of *Bothriolepis* cf.*trautscholdi* associated with *Psammosteus megalopteryx, Holonema radiatum* and undetermined sarcopterygian elements, are reported from the Porkhov and Svinord Beds. A similar assemblage is also reported from the Il'men' Beds. Fish remains are practically absent in the Buregi Beds. The vertebrates of the assemblage from the dolomites of the Al'tova Beds, exposed at the left bank of Gauja River near Vidaga village, are represented by mostly poorly preserved, usually deformed plates of the head-shield, trunk and pectoral armour of *Bothriolepis trautscholdi* Jaekel, fragments of the branchial and dorsal shield of *Psammosteus megalopteryx* (Trautschold), scales of the porolepiform sarcopterygian *Holoptychius* cf.*nobilissimus* Ag. and skull bones of a eusthenopterid sarcopterygian conforming to *Jarvikina wenjukovi* (Rohon).

The deposits of the S n e z h a Regional Substage in the eastern part of the Main Devonian Field are represented mainly by variegated facies and consists of carbonate clays and siltstones with thin layers of sandstones and limestones. The Snezha Regional Substage consists of the Katleši Formation and Kuprava Beds in most complete sequences all over the Main Devonian Field. Several levels of the clays and dolomite sandstones of the Katleši Formation contain a quantitatively rich vertebrate assemblages. One of the well-known sites is located at the right bank of Daugava River 20-50 m upstream from the mouth of Ranka River not far from ruins of Lielvārde castle (Sorokin et al., 1981). Abundant disarticulated plates of the armour and articulated head-shields of *Bothriolepis maxima* Gross, rare indeterminable remains of a small *Bothriolepis* sp., branchial plates of *Psammosteus falcatus* Gross and rare scales of *Holoptychius* cf.*nobilissimus* are collected from the light silty sandstone and orange-brown sandstone with dolomite cement in layer 11 of this locality. *B.maxima* is recorded also from the Jêkabpils quarry (lower part of the Katleši Formation), exposures at Liepna River 2 km W from Katleši village and from clays of Kuprava quarry (Sorokin, 1978).

P a m ū š i s Regional Substage comprises the Pamūšis Formation in Lithuania, Ogre Formation in Latvia and Prilovat' Formation (previous Nadsnezha Beds) in eastern part of the Main Devonian Field. The deposits of the Pamūšis Formation , consisting mainly of sandstones, clays, marls and dolomites, contain fish remains in the lower part of sequence, usually only in sandstones. *Bothriolepis maxima* usually dominates the assemblage; remains of this species were found in the sites at the left bank of Nemunėlis River near Pakalniečiai village and in the vicinity of Didžpanemunis; borehole Stačiūnai, 139.4-139.7 m deep and borehole Petrašiūnai, 57.8-58.0 m deep. The sandstones and sandy dolomites composing the Ogre Formation yeild a richer assemblage, containing several antiarch species. Vertebrates of the Ogre Formation are diverse and represented by the heterostracans *Psammosteus falcatus, P.tenuis* Obr. and *Aspidosteus heckeri* Obr., the placoderms *Asterolepis? amulensis* Lyarska¸a, *Bothriolepis maxima, B.evaldi* Lyarska¸a, *Grossilepis spinosa* (Gross) and *Taeniolepis speciosa* Gross, the acanthodian *Devononchus laevis* Gross, the sarcopterygians *Holoptychius* cf.*nobilissimus* Ag., *Platycephalichthys bischoffi* Vorob., *Eusthenodon* sp. and *Dipterus* cf.*marginalis* Ag., and the possible tetrapod *Obruchevichthys gracilis* Vorob. *Bothriolepis maxima* is the most widely distributed species of antiarch in this assemblage. It has been found in the well-known locality Velna Ala: cave and outcrop of light grey sandstones at the left bank of Abava River; exposure at the left bank of Imula River not far from Kalnarāji hamlet; in the vicinity of Ceraukste at Mūsa River; and in outcrops along Ogre River. *Bothriolepis evaldi* was recorded only from two localities: mostly disarticulated plates of the armour and only one articulated head-shield come from thin a layer of the light blue siltstone in between grey sandstones at the right bank of Kaibala River 200 m from estuary, and very well preserved complete armours of small fishes were collected by Lyarskaya from grey silty sandstones of the Rembate Member (lower part of the Ogre Formation) exposed at the left bank of Amula River 0.3 km downstream from Kalnamuiža watermill. The only known specimens of *Grossilepis spinosa* are described and illustrated by Gross (1942) from the Velna Ala locality. The Prilovat' Formation deposits are exposed mainly in the basin of Lovat' River in Novgorod region of Russia, along Lovat', Kun'ya, Bolshoy Tuder River, as well as at rivers Msta, Pasha etc. Well preserved vertebrate remains were gathered by D.Obruchev from several localities along Lovat' River north from Holm town: near Luka village and Kurskoye Gorodische among others. All this material is kept at the PIN. The vertebrate assemblage closely resembles that from the Ogre Formation and consists of *Psammosteus falcatus, Aspidosteus heckeri, Bothriolepis maxima, Bothriolepis* sp., *Devononchus laevis, Holoptychius* cf.*nobilissimus, Platycephalichthys bischoffi, Eusthenodon* sp. and *Dipterus* cf.*marginalis*. A quite similar assemblage was reported from the outcrops along Verkhnyaya Paluitsa and Nizhnyaya Paluitsa River (tributaries of Pasha River, Tikhvin district of Leningrad region), comprising *Bothriolepis maxima, Devononchus laevis, Haplacanthus* sp., *Holoptychius nobilissimus, Holoptychius giganteus* Ag., *Panderichthys* sp., *Platycephalichthys bischoffi, Onychodus* sp. and *Dipterus* sp. (Ivanov, Khozatski, 1986). The fish remains are usually poorly preserved and bears traces of abrasion. Some taxa characteristic for the Snezha - Pamūšis vertebrate assemblage were reported from the Lyaiol' and the Sirachoy Formations of South Timan, the Kamennyy Ruchey Formation of Middle Timan and the Kamennyy Formation of North Timan.

Vertabrates are absent in the Imula and Bauska Beds of the S t i p i n a i Regional Substage (in western part of the Main Devonian Field) and are scarce in the Smota Beds, which contains no *Bothriolepis*.

A m u l a Regional Substage is subdivided into the Pakruojis Formation in Lithuania, Amula Formation in Latvia and Nadsmota Beds in Russia (Sorokin et al., 1981). It is distributed in Baltic region only in the southern part of Western Latvia and North-Western Lithuania and comprises sands and sandstones with layers of siltstones and silty dolomites, which contain the remains of vertebrates, lingulid shells and ichnofossils, changing with facially variable clays, clayey siltstones, dolomite marls and unfossiliferous dolomites. The Amula Formation is usually subdivided into three members (Sorokin et al., 1981); the Lower and Upper Amula Members contain vertebrate remains. The deposits of the Amula Formation are well exposed in the stratotype at the left bank of Amula River upstream from Kalnamuiža watermill. Fish and agnathan plates, teeth and scales from the Lower Amula Member are often poorly preserved. The assemblage is taxonomically not diverse yielding *Psammosteus tenuis*, abundant *Devononchus laevis, Holoptychius* cf.*nobilissimus*, and undetermined *Bothriolepis*, chondrichthyan and dipnoan remains. The Upper Amula Member fish assemblage differs clearly from the latter in the absence of psammosteids, presence of *Bothriolepis curonica* Gross, the acanthodian *Haplacanthus* sp., and osteolepiform and struniiform sarcopterygians, as well as some other taxa. As the vertebrate assemblage and spores of the Upper Amula Member show great similarities with that of the Famennian Eleja Formation, is would possibly be more correct to equate the Upper Amula Member to the Eleja Regional Substage.

The Kruoja and Šiauliai Formations in Lithuania and Eleja Formation of Latvia, united into the E l e j a Regional Substage, 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 Eleja Formation is subdivided into Purviņi, Sesava and Cimmermaņi

Members. The lower, Purviņi Member is composed mostly of clays with thin layers of sandstones, sometimes of clayey dolomites or dolomite marls. The aforementioned vertebrate assemblage with dominant *Bothriolepis curonica* is represented in two localities: in the stratotype section of the Amula Formation and in the site at the right bank of Imula River near Bienes hamlet. Abundant articulated head-shields and pectoral fins, separate plates of the trunk armour of *Bothriolepis curonica*, rare scales of *Holoptychius*, spines and scales of the acanthodian *Devononchus*, struniiform fish teeth, scales of dipnoans and rare palaeoniscids are usually slightly deformed and, apart from the remains of *Bothriolepis*, of poor preservation.

The Joniškis Formation of Lithuania and Latvia corresponds to the J o n i š k i s Regional Substage. The ichthyofauna of the Joniškis Formation is very scarce and contain mostly microremains of acanthodians, struniiforms, dipnoans, actinopterygians and macroremains of "*Dinichthys*", mentioned, but not figured by O.Obrucheva. This interval probably corresponds to the Chimayevsk Formation of the eastern part of the Main Devonian Field.

K u r s a Regional Substage and the Kursa Formation, respectively, are distributed in the southern part of Western Latvia and North-Western Lithuania and comprise limestones in their western part, with increasing degree of dolomitization and quantity of clastic material to the east. The limestones yield a rich and diverse invertebrate assemblage consisting of bryozoans, crinoids, brachiopods, worms, bivalves and gastropods. Microremains of acanthodians, sarcopterygians, actinopterygians and recently-found elasmobranchs (Ivanov, Lukševičs, 1994), as well as macroremains of *Phyllolepis* were recorded from Kursa Formation dolomites, mostly borehole material. The Tuder Beds of the eastern part of the Main Devonian Field probably corresponds to the main part of this interval.

A k m e n e Regional Substage 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 dolomites with thin layers of sandstones, siltstones and clays. The dolomites contain a diverse assemblage of marine invertebrates, such as brachiopods, bivalves, bryozoans, crinoids and worms, as well as the remains of fishes. Apart from *Phyllolepis*, the remains of undeterminable *Bothriolepis*, the ptyctodontid *Chelyophorus*, the acanthodian *Devononchus*, struniiform teeth, macroremains of *Megapomus heckeri* Vorob. and actinopterygian scales are found there. Fish remains from the Bilovo Beds, which are usually interpreted as corresponding to the Akmene Formation, are poorly known, but contain a new species *Bothriolepis heckeri* with a high crest on the dorsal wall of the trunk armour.

The M ū r i Regional Substage contains the Mūri Formation, occuring in Latvia and Lithuania, and the Tērvete Formation, distributed only in Latvia. The sandstones, sands and carbonate sandstones with thin layers of coquinas of the Mūri Formation usually contain well preserved shells of brachiopods, bivalves, gastropods, nautiloids, crinoids remains and vertebrates. The layers of sands and sandy-clayey deposits usually yield no organic remains. Recent research, carried out as a contribution to IGCP project 328, has increased the number of known taxa in the vertabrate assemblage from the Mūri Formation to ten species. The placoderms *Bothriolepis jani* Lukševičs, *Chelyophorus* sp. and an undetermined dinichthyid, the acanthodian *Homacanthus sveteensis* Gross, protacrodontid and stethacanthid chondrichthyans, struniiform, osteolepid and dipterid sarcopterygians and palaeoniscids were found in the outcrop of sandstones at the right bank of Svēte River near Ķurbes hamlet; a fairly similar assemblage is known from exposures at the right bank of Šķēde River in vicinity of Omiķi hamlet. A new discovery of a chondrichthyan-acanthodian-actinopterygians fauna in one layer together with a porolepiform-osteolepiform-antiarchs association is of special interest. The Tērvete Formation, comprising white and light pink sands, dolomite marls and siltstones, yields the most diverse fish assemblage of Upper Famennian age. Sands exposed on the right bank of Skujaine River, not far from Klūnas village, contain well preserved abundant disarticulated bones of two antiarch species: *Bothriolepis jani* and *B.ornata* Eichw.; three other placoderm taxa: *Phyllolepis tolli* Vasiliauskas, *Chelyophorus* sp. and a undetermined dinichthyid; rare spines and scales of two acanthodians, *Homacanthus sveteensis* and *Devononchus tenuispinus* Gross; bones, scales and teeth of *Holoptychius* cf.*nobilissimus*, *Cryptolepis* sp. and *Platycephalichthys skuenicus* Vorob.; two types of dipnoan tooth plates (*Conchodus* and "*Dipterus*"); and scales of actinopterygians. A vertebrate assemblage similar to that of the Tērvete Formation was reported from the upper part of the L'nyanka Formation (Ostrometskaya, Kotlukova, 1966), from the localities at Mshanka and L'nyanka Rivers in Novgorod region. *Bothriolepis ornata* is known also from the outcrops at Priksha River (Eichwald, 1860) and along the Msta River (Obruchev, 1964).

Š v ē t e Regional Substage corresponds to the Švēte Formation in Lithuania and Sniķere Formation in Latvia. According to Žeiba and Valiukevičius (1972: in Sorokin et al., 1981), it probably corresponds to the *postera* conodont zone; the boundary between previously used lower *styriacus* - middle *styriacus* conodont zones is traced within the Švēte Formation. This formation contains sandstones, clays and siltstones in its lower part and sandstones, sandy dolomites, dolomite marls and siltstone in upper part. Scarce remains of brachiopods, bivalves, conodonts and fishes have been reported from it. In Latvia the Sniķere Formation is characterized by more widely represented calcareous deposits, containing brachiopods, bivalves, gastropods, crinoids, ichnofossils and vertebrates. The fish assemblage is not very diverse, yielding usually poorly preserved remains of undeterminable *Bothriolepis*, the ptyctodontid *Chelyophorus*, the acanthodian *Homacanthus sveteensis*, *Platycephalichthys skuenicus* and struniiform sarcopterygians and palaeoniscids.

The Žagare Formation of the Ž a g a r e Regional Substage is distributed both in Lithuania and Latvia. It is represented mostly by dolomites or sandy dolomites with concentrations of brachiopod shells and crinoids. Vertebrate remains are rare, usually occuring in sandstones with strong dolomite cement. Poorly preserved fragments of *Bothriolepis*, *Chelyophorus*, an undeterminated dinichthyid, some osteolepiform, struniiform and dipterid sarcopterygians and palaeoniscids are found in the yellow sandy dolomites exposed in the Skaistgiris quarry in Lithuania.

K e t l e r i Regional Substage and Ketleri Formation, respectively, are distributed in a relatively small territory of south-western part of Latvia and north-western part of Lithuania, comprising sands, sandstones, clays and dolomite marls. It is subdivided into three subformations (Lyarskaya & Savvaitova, 1974). The lower subformation contains mostly clayey-calcareous deposits, which in the sections in Lithuania contain fragments of poorly preserved fishes with *Chelyophorus* sp. among them. Probably the same assemblage, including undeterminable *Bothriolepis* and *Chelyophorus*, is reported from the localities along Venta River in vicinity of Lienas village in Latvia (Sorokin et al., 1981). The middle and upper subformations are well represented in the well-known localities at the left bank of Ciecere River downstream from Pavāri hamlet and at the right bank of Venta River not far from Ketleri hamlet (Lyarskaya & Savvaitova, 1974; Lukševičs, 1991). Both of the sites are characterized by a rich fish and primitive tetrapod assemblage (Lukševičs, 1991; Ahlberg et al., 1994) which includes the placoderm *Bothriolepis ciecere* Lyarskaja, the acanthodians *Devononchus tenuispinus* and *D.ketleriensis* Gross, the porolepiform *Holoptychius* cf.*nobilissimus*, the osteolepiforms *Cryptolepis grossi* Vorob., *Glyptopomus? bystrowi* (Gross) (determined by Lebedev, 1995) and an undetermined eusthenopterid, the dipnoan *Orlovichthys* cf.*limnatis* Krupina, the unusual sarcopterygian *Ventalepis ketleriensis* Schultze and two taxa of tetrapods: *Ventastega curonica* Ahlberg, Lukševičs & Lebedev and undetermined other primitiv amphibian.

The wide geographical and relatively narrow stratigraphical distribution of the species of *Bothriolepis* makes it possible to use the species of this genus in the vertebrate zonation of the Upper Devonian of the East European Platform (Rzhonsnitskaya, Kulikova, 1990). Two *Bothriolepis*-based zones for the Upper Devonian of Baltic region were proposed for the first time by Lyarskaya (1978). She suggested the ***prima*** and ***obrutschewi*** vertebrate zones for the lower and upper parts of the Amata Regional Substage, respectively (***Bothriolepis prima*** and ***B.obrutschewi*** zones in the original transcription) and described the vertebrate assemblages of the overlying levels without indication of zones. Later Lyarskaya and Talimaa (Rzhonsnitskaya, 1988) extended the zonation into both Frasnian and Famennian, but without the formal description of zones. Ivanov (1993) proposed a new zonation of the Frasnian for the East European Platform, and also specified the extent of some previously known zones. The vertebrate zonation of the Famennian of the Main Devonian Field was analized by Lukševičs (1995).

The vertebrate zonation based on the stratigraphic ranges of *Bothriolepis* is proposed for the mostly shallow-water facies, rich in terrigenous deposits, of the Main Devonian Field. Zonal assemblages of vertebrates contain taxa with different stratigraphical ranges. The characteristic taxa (or associated taxa) are restricted to one zone only. The transitional species appear in the previous zone (zones) and: disappear in the zone under description (old transitional taxa), extent into the following zone; or appear in the zone under description and range into the next zone (young transitional taxa). The zone is proposed as biozone in cases when it corresponds to the full range of index-taxon and as interval zone, when it occupied a part of range of the latter.

Prima* - *obrutschewi biozone. Index taxa: *Bothriolepis prima* Gross and *Bothriolepis obrutschewi* Gross.
Lower limit: first occurence of *Bothriolepis prima*.
Upper limit: first occurence of *Bothriolepis cellulosa* (Pander).
Corresponding stratigraphic unit: Amata Regional Substage, probably Frasnian.
Remarks: Associated taxa: *Psammosteus cuneatus, P.livonicus, P.levis, Eusthenopteron obruchevi*. Several young transitional taxa, such as *Psammosteus maeandrinus, P. praecursor, Asterolepis radiata* appear in this zone. As it is difficult to determine the precise upper limit of the previously described ***prima*** zone (Lyarskaya, 1978), the ***prima*** and overlying ***obrutschewi*** zones are usually used together for correlation of strata and united therefore here.

Cellulosa biozone. Index taxon: *Bothriolepis cellulosa* (Pander).
Lower limit: first occurence of *Bothriolepis cellulosa*.
Upper limit: last occurence of *Bothriolepis cellulosa*.
Corresponding stratigraphic unit: Snetnaya Gora and Pskov Beds of the Pļaviņas Regional Substage, Frasnian.
Remarks: ***Cellulosa*** zone contains a lot of associated taxa: *Bothriolepis panderi, Grossilepis tuberculata, Ctenurella pskovensis, Plourdosteus mironovi, Haplacanthus perseensis, Latvius grewingki, Eusthenopteron saevesoederberghi, Strunius rolandi, Rhinodipterus secans, Griphognathus minutidens* and *Moythomasia perforata*, as well as some old transitional taxa such as *Psammosteus maeandrinus* and *Asterolepis radiata*. The overlying Chudovo Beds yeilds scarce vertebrate remains of some of associated taxa.

Trautscholdi interval zone. Index taxon: *Bothriolepis trautscholdi* Jaekel.
Lower limit: first occurence of *Bothriolepis trautscholdi*.
Upper limit: first occurence of *Bothriolepis maxima*.
Corresponding stratigraphic units: Dubnik and Daugava Regional Substages, Frasnian.
Remarks: Associated taxa: *Psammosteus megalopteryx, P.pectinatus, Gyroplacosteus panderi, Plourdosteus trautscholdi, Eastmanosteus egloni, Asterolepis syasiensis, Jarvikina wenjukovi, Parapanderichthys stolbovi.*

Maxima biozone. Index taxon: *Bothriolepis maxima* Gross.
Lower limit: first occurence of *Bothriolepis maxima*.
Upper limit: last occurence of *Bothriolepis maxima*.
Corresponding stratigraphic units: Snezha and Pamūšis Regional Substages, Frasnian.
Remarks: Some of associated taxa, such as *Psammosteus falcatus, Aspidosteus heckeri* and *Platycephalichthys bischoffi*, have a similar range as an index taxon; some other taxa have been reported only from the Pamūšis Regional Substage: *Bothriolepis evaldi, Grossilepis spinosa, Taeniolepis speciosa, Obruchevichthys gracilis*. Because vertebrates are practically absent or poorly preserved in the Stipinai and Amula Regional Substages, it is very difficult to establish the vertebrate zone for this interval.

Unzoned interval.
Corresponding stratigraphic units: Stipinai and Amula Regional Substages, Frasnian.

Curonica interval zone. Index taxon: *Bothriolepis curonica* Gross.
Lower limit: first occurence of *Bothriolepis curonica*.
Upper limit: first occurence of *Phyllolepis*.
Corresponding stratigraphic units: probably from Eleja to Joniškis Regional Substage, Famennian.
Remarks: *Bothriolepis* remains are scarce in Kursa and Akmene Regional Substages, therefore the genus *Phyllolepis* is selected as an index taxon for this very broad vertebrate zone.

Phyllolepis biozone. Index taxon: genus *Phyllolepis*.
Lower limit: first occurence of *Phyllolepis*.
Upper limit: last occurence of *Phyllolepis*.
Corresponding stratigraphic units: from the Kursa Regional Substage to the Mūri Regional Substage, Famennian.

Remarks: *Bothriolepis* remains are scarce in the Kursa and Akmene Regional Substages, but abundant in overlying Mūri Regional Substage. Therefore the establishing of the ***ornata*** vertebrate zone, proposed by Mark-Kurik (pers.comm.), is supported here.

Ornata biosubzone. Index taxon: *Bothriolepis ornata* Eichw.
Lower limit: first occurence of *Bothriolepis jani*.
Upper limit: last occurence of *Bothriolepis ornata.*
Corresponding stratigraphic unit: Mūri Regional Substage, Famennian.
Remarks: Some associated taxa, such as *Phyllolepis tolli* and *Bothriolepis jani*, have more wide distribution within this zone than that of the index taxon. Young transitional taxa *Homacanthus sveteensis, Devononchus tenuispinus* and *Platycephalicthys skuenicus* appear there. The whole of this zone lies within the limits of the broad *Phyllolepis* zone.

Unzoned interval.
Corresponding stratigraphic units: Švete and Žagare Regional Substages, Famennian.
Remarks: Because the Švete and Žagare Regional Substages yeild a scarce remains of undeterminable *Bothriolepis*, it is difficult to establish the vertebrate zone for this interval. Some old transitional species extent into this interval.

Ciecere biozone. Index taxon: *Bothriolepis ciecere* Lyarskaya.
Lower limit: first occurence of *Bothriolepis ciecere*.
Upper limit: last occurence of *Bothriolepis ciecere.*
Corresponding stratigraphic unit: the upper part of the Ketleri Regional Substage, Famennian.
Remarks: Associated taxa: first occurence of *Devononchus ketleriensis*, *Cryptolepis grossi*, *Glyptopomus? bystrowi*, *Ventalepis ketleriensis*, *Ventastega curonica*.
Because the overlying formations in Baltic sequence contain only scarce remains of sarcopterygians and actinopterygians, the vertebrate zonation of the Main Devonian Field ends with the ***ciecere*** vertebrate zone.

The proposed vertebrate zonation is useful not only in the Main Devonian Field, but also in adjacent teritories, for example in Timan province (Ivanov, Lukševičs, in press), where the most part of the Frasnian zones could be traced and correlated with the standard conodont zonation. The conodont distribution in the Main Devonian Field is poorly known as yet. Using the distribution of the vertebrate assemblages and conodonts in the Timan it is possibly to make a preliminary correlation of the Vertebrate Zonation with the Standard Conodont Zonation (Ivanov, Lukševičs, in press). Conodont data were reported from the South and Middle Timan sections, providing the possibility to correlate them with the new

Standard Conodont Zonation (Kuzmin, 1995; Ziegler & Sandberg, 1990). It thus became possible to try to find a relationship between the vertebrate assemblages of the Timan regions to ichthyozonation of the Main Devonian Field on the one hand, and the Standard Conodont Zonation on the another.

Only two vertebrate zones could be traced in the Frasnian of the South Timan, where deep water deposits dominate the sections. The first, the ***cellulosa*** zone corresponding to the Pļaviņas Regional Substage of the Main Devonian Field, which is widely distributed on the East European Platform (Ivanov, 1993), corresponds to the Upper Timan - Lower Ust'e Yarega stratigraphic interval. The ***maxima*** zone (Snezha and Pamūšis Regional Substages of the Main Devonian Field) was reported from the Sirachoy and Lyaiol Formations, the latter yielding *Psammosteus falcatus*. However, the most of the conodont zones were recognized in the South Timan sections, and the ***Phoebodus bifurcatus*** zone of a new phoebodont based ichthyolith zonation (Ginter & Ivanov, 1995) is placed in the Lyaiol Formation. The ***falsiovalis*** zone of the new Standard Conodont Zonation can probably be correlated with the Upper Timan Formation and Lower and Middle Ust'e Yarega Members (Kuzmin, 1995). The ***transitans*** zone corresponds possibly to the Upper Ust'e Yarega Member. The Domanik Formation corresponds to the three Standard Conodont zones starting with the ***punctata*** to ***jamieae*** zones. Both the Vetlasyan and Sirachoy Formations could be correlated with the **early *rhenana*** zone, but the Ukhta Formation correlates with **late *rhenana* - *linguiformis*** zones. The Savinobor Formation probably corresponds to the ***triangularis*** zone.

At present only three levels corresponding to the conodont zonation could be found in the Frasnian Middle Timan sections and three vertebrate zones were reported from there. The ***prima* - *obrutschewi*** zones (Amata Regional Substage of probably Frasnian age of the Main Devonian Field) corresponds to the Ust'e Chirka Formation and the ***cellulosa*** zone is correlated with the lower part of the Ust'e Yarega Formation. The Kamennyy Ruchey Formation contains the vertebrate assemblage of the ***maxima*** zone.

Three Frasnian and one Famennian vertebrate zones were recognized in the North Timan sequence: the ***prima* - *obrutschewi*** zones in the Kumushka Formation, the ***trautscholdi*** zone (Dubnik and Daugava Regional Substages of the Main Devonian Field), possibly in the Ust'e Bezmoshitsa Formation, the ***maxima*** zone in the Kamennyy Formation and the ***ornata*** subzone probably in the Pokayama Formation.

Summing up one could say the ***prima* - *obrutschewi*** zones can probably be corresponded to the part of **early *falsiovalis*** - **late *falsiovalis*** zones. The ***cellulosa*** zone could be correlated with the part of the same conodont zone. The ***maxima*** zone could be well correlated with the upper part of **early *rhenana*** zone. According to Žeiba and Valiukevičius (1972: in Sorokin et al., 1981) and data of Kuzmin (in press) the Eleja Formation and lowermost part of the Joniškis Formation could be correspond to the ***early*** -

Table 20. Vertebrate zonation and correlation of the Upper Devonian of the Main Devonian Field

Series	Stage	Standard Conodont Zonation		Vertebrate zonation	Regional Substages, beds of the Main Devonian Field	
UPPER DEVONIAN	Famennian					
		expansa		*ciecere*	Ketleri	
				unzoned interval	Žagare	
		postera			Švėtė	
		trachytera		*Phyllolepis* *ornata*	Mūri	Tērvete Mūri
		marginifera			Akmene	
		rhomboidea *crepida*			Kursa	
		triangularis	Upper Middle	*curonica*	Joniškis	
			Early		Eleja	
	Frasnian	*linguiformis*		unzoned interval	Amula	
		rhenana	Upper		Stipinai	
			Early	*maxima*	Pamušis	
		jamieae			Snezha	
		hassi	Upper Early	*trautscholdi*	Daugava	Altovo Buregi Il'men' Svinord Porkhov
		punctata			Dubnik	
		transitans		unzoned interval *cellulosa*	Pļaviņas	Chudovo Pskov Snetnaya Gora
		falsiovalis	Upper Early	*obrutschewi - prima*	Amata	

middle triangularis and ***upper triangularis*** conodont Zones, respectively. Consequently, the ***curonica*** zone corresponds to the ***triangularis*** and probably the lower part of ***crepida*** conodont zones. As the Švete Regional Substage contains the conodonts of ***postera*** zone (Žeiba & Valiukevičius, 1972: in Sorokin et al., 1981), the upper limit of the ***ornata*** vertebrate subzone could probably be traced from the ***upper trachytera*** to ***early postera*** conodont zones.

Summary

1. About 150 years long study of bothriolepid placoderms from the north-western part of the East European Platform is resulted in establishing of several taxa. Now 16 species or unnamed forms of specific level are known from the Main Devonian Field and described above: *Bothriolepis prima* Gross, *B.obrutschewi* Gross, *B.cellulosa* (Pander), *B.panderi* Lahusen, *B.trautscholdi* Jaekel, *B.maxima* Gross, *B.evaldi* Lyarskaja, *B.curonica* Gross, *Bothriolepis heckeri* sp.nov., *B.ornata* Eichwald, *B.jani* Lukševičs, *Bothriolepis* sp.indet.1, *Bothriolepis* sp.indet.2, *B.ciecere* Lyarskaja, *Grossilepis tuberculata* (Gross), *G.spinosa* (Gross).

2. The previously described species of *Bothriolepis* have been critically treated. The name *Bothriolepis favosa* Agassiz is rejected from the list of valid specific names as based on the porolepiform (?) lower jaw. *Bothriolepis pavariensis* Lyarskaja recently was mentioned by the author (Lukševičs, 1991) to be synonymous to *B.ciecere* Lyarskaja. The remains of bothriolepid from Syas' River are referred here to a species *B.trautscholdi* established by Jaekel and claimed by Gross as synonymous to *B.panderi* Lahusen.

3. Four new forms are described here: previously established *Bothriolepis jani* Lukševičs (1986), a new species *B.heckeri* and two unnamed forms from the eastern part of the Main Devonian Field as too poorly known.

4. The interrelationships of the various Antiarchi-forms have been discussed and position of some previously described taxa is precised. *Asperaspis carinata* Panteleyev from the Middle Devonian of Central Kazakhstan is placed within Pterichthyodidae. *Tenizolepis* Malinovskaya from Kazakhstan and *Kirgizolepis* Panteleyev from Kirgizia previously described as belonging to Bothriolepididae are referred to Dianolepididae.

5. The variability of several bothriolepids is analyzed using correlation and regression analysis, as well as a new statistic method recently proposed by V.Cherepanov (1986). 754 specimens of 9 taxa of *Bothriolepis* and *Grossilepis tuberculata* were measured, then indices of measurements, regression coefficients, correlation coefficients and Cherepanov's parameters were calculated. Regression analysis seems to be a good tool for determination of the growth pattern, and correlation analysis is useless for phylogenetic purposes in studying antiarchs. The results of the analysis of continuous variability of investigated bothriolepids obviously demonstrate the possibilities of Cherepanov's method in recognition of species.

6. The analysis of the importance of several features for the recognition of species allowed to select ten indices showing the significant differences between separate species in more than 70 per cent of compared pairs of species: LPrm/WrPrm, WAMD/WaAMD, LtAMD/LAMD, LADL/WADL, LMxL/WMxL, WNu/TNu, LHs/LPrm, WrPrm/WoPrm, LMxL/HMxL, WOf/WHs.

7. The tentative hypothesis on interrelationships of bothriolepids from the Main Devonian Field is proposed on the base of statistic analysis results using all the quantitative morphological features. Four groups could be recognized within this family: the first one is a group of two species of *Grossilepis*, which differs well from all representatives of genus *Bothriolepis*. The second is characterized by a low and broad trunk armour and comprises only Frasnian species *Bothriolepis obrutschewi*, *B.cellulosa*, probably *B.panderi*, *B.trautscholdi* and *B.maxima*. Other characteristic feature of this group is the increasing of size of individuals in time. *B.evaldi* and *B.jani*, a small fishes with relatively high dorsal wall of the trunk armour are composing a third group, probably derived from *B.cellulosa*. The last group includes *B.curonica*, *B.ornata* and *B.ciecere* with relatively low, long and narrow trunk armour which were possibly better swimmers than a members of the above mentioned group.

8. Bothriolepids are characterized by wide geographical distribution, such species as *Bothriolepis obrutschewi* and *B.cellulosa* were reported both from the Main Devonian Field and Timan, and some forms show a great similarities with species distributed in Timan, Scotland, East Greenland and Canada. All bothriolepids from the north-western part of East European Platform differ well from the representatives of this family from Kazakhstan, China, Australia and Antarctic.

9. The stratigraphic distribution of bothriolepids through the Upper Devonian of the Main Devonian Field is precised and a new vertebrate base zonation for this interval is proposed here. ***Prima*, *obrutschewi*, *cellulosa*, *trautscholdi*, *maxima*, *curonica*, *ornata*** and ***ciecere*** zones, based on the distribution of *Bothriolepis* species, and ***Phyllolepis*** zone correspond to an almost all the Regional Substages of the Main Devonian Field. The preliminary correlation of proposed vertebrate-based zones with the Standard Conodont zonation is made on the base of the analysis of vertebrate distribution in the Main Devonian Field and Timan, as well as distribution of conodonts in the South and Middle Timan.

Localities

The following list provides details of all localities of the Main Devonian Field studied by the author and mentioned in the text. The list also includes several localities described or mentioned elsewhere in case *Bothriolepis* remains were available for reexamination.

KETLERI (1) Latvia, Kuldīga district, approximately 3 km to the south from Lēnas village. An outcrop exposing light sands and sandstones at the right bank of Venta River 1 km W from Ketleri hamlet. Stratotype of the upper Member (Varkaļi) of the Ketleri Formation. Upper Famennian. *Bothriolepis ciecere.*

PAVĀRI (2) Latvia, Saldus district, approximately 10 km E from Skrunda City. Light-coloured sands, sandstones, siltstones, clays and dolomite marls of the middle Member (Airītes) of the Ketleri Formation are exposed at the left bank of Ciecere River downstream from the Pavāri hamlet. Upper Famennian. *Bothriolepis ciecere.*

BIENES (3) Latvia, Tukums district, approximately 10 km W from Kandava City, 500 m SW from Bienes hamlet. Outcrop of sandstones of the Amula Formation and lower part of the Eleja Formation on the right bank of Imula River. Upper Frasnian - Lower Famennian. *Bothriolepis curonica* (in Eleja Formation).

KALNARĀJI (4) Latvia, Tukums district, approximately 9 km W from Kandava City, down Kalnarāji hamlet. Exposure # 346 of hard light grey Ogre sandstones near estuary of Imula River. Upper Frasnian. *Bothriolepis maxima, Asterolepis? amulensis.*

KALNAMUIŽA 1 (5) Latvia, Tukums district, approximately 7 km W from Kandava City. Cliff at the left bank of Amula River down water-mill Kalnamuiža with grey sandstones and bluish marls of the Ogre Formation. Upper Frasnian. *Bothriolepis evaldi.*

KALNAMUIŽA 2 (6) Latvia, Tukums district, approximately 7,5 km W from Kandava City. Stratotype of Amula Formation at the right bank of Amula River 1 km up from water-mill Kalnamuiža. Contains Bauska Beds of Stipinai Formation; rhythmic intercalation of sands and sandstones containing fish remains with multicoloured clays, siltstones, dolomite marls and thin-layered dolomites of Amula Formation; dolomite marls, clays and siltstones of Eleja Formation. Upper Frasnian - Lower Famennian. *Bothriolepis sp.* (in yellow sandstones of Amula Formation), *Bothriolepis curonica* (in blue clays of Eleja Formation).

VELNA ALA (7) Latvia, Tukums district, approximately 6 km W from Kandava City. Outcrop and caves composed by light grey sandstones of the Ogre Formation on the left bank of Abava River. Upper Frasnian. *Bothriolepis maxima, Grossilepis spinosa.*

KLŪNAS (8) Latvia, Dobele district, 10 km W from Tērvete. Stratotype and neighbouring exposure of white and pink sands containing abundant fish bones, dolomite marls and marls of the Tērvete Formation on the right bank of Skujaine River down Klūnas village. Upper Famennian. *Bothriolepis ornata, B.jani.*

ĶURBES (9) Latvia, Jelgava district, 2 km W from Mūrmuiža. Outcrop of red and pink sandstones of the Mūri Formation on the right bank of Svēte River near Ķurbes hamlet. Upper Famennian. *Bothriolepis jani*.

CERAUKSTE (10) Latvia, Bauska district, Ceraukste village. Outcrop of sandstones of the Ogre Formation at Mūsa River. Upper Frasnian. *Bothriolepis maxima*.

LIELVĀRDE (11) Latvia, Ogre district, Lielvārde. Stratotype of the Katleši Formation, exposures # 199 and 199a at the right bank of Daugava River near Lielvārde castle. Deposits consist of sandstones, clays, marls and dolomites. Middle Frasnian. *Bothriolepis maxima, Bothriolepis sp.*

KAIBALA (12) Latvia, Ogre district, approximately 4 km SE from Lielvārde. Cliff consisting of grey sanstones and thin layers of blue marls of Ogre Formation at the right bank of Kaibala River 200 m from estuary. Upper Frasnian. *Bothriolepis evaldi*.

KOKNESE (13) Latvia, Aizkraukle district, near Koknese City. Outcrop of dolomites, dolomite marls and clays of Snetnaya Gora Beds (Pļaviņas Formation) at the right bank of Daugava River (now under the water). Lower Frasnian. *Bothriolepis cellulosa, Grossilepis tuberculata*.

PASTAMUIŽA (14) Latvia, Aizkraukle district, 1.5 km upstream the ruins of Koknese castle. Outcrop of mostly sandstones, siltstones and clays of Amata Formation and dolomite marls of Pļaviņas Formation on the left bank of Daugava River (now under the water level). Upper Givetian (?) - Lower Frasnian. *Bothriolepis prima*: in redish-brown sandstones; *B.obrutschewi*: in white sandstones of Amata Formation; *B.cellulosa*: in Pļaviņas Formation.

JĒKABPILS (15) Latvia, Jēkabpils district, Jēkabpils City. Quarry of dolomites of Katleši Formation. *Bothriolepis sp.*

PELYŠA (16) Lithuania, Anykščiai district. Outcrops of the sandstones, siltstones and clays at the right bank of Pelyša River, right tributary of Šventoji River. *Bothriolepis prima, B.obrutschewi*.

VIDAGA (17) Latvia, Alūksne district, approximately 3 km S from Vireši. Exposure # 548 of the Altovo Beds of the Daugava Formation at the left bank of Gauja River not far from Vidaga village, with dolomites containing fish remains. Middle Frasnian. *Bothriolepis trautscholdi*.

KATLEŠI (18) Latvia, Balvi district, 2 km W from Katleši. Exposure # 508 at the right bank of Liepna River, the Katleši Formation. Middle Frasnian. *Bothriolepis maxima*.

KUPRAVA (19) Latvia, Balvi district, Kuprava village. Large quarry for mining clays of the Kuprava Beds of the Katleši Formation. Middle Frasnian. *Bothriolepis cf.maxima*.

PISKOVICHI (20) Russia, Pskov region, Pskov City. Cliff at the right bank of Velikaya River with deposits of the Amata and Pļaviņas Formations. Upper Givetian (?) - Lower Frasnian. *Bothriolepis obrutschewi*.

YAM-TESOVO (21) Russia, Leningrad region. Outcrop at Oredezsh River. Staritsa Beds of the (?) Upper Givetian - Lower Frasnian. *Bothriolepis prima* in yellow-grey sandstone.

KURSKOYE GORODISHCHE (22) Russia, Novgorod region, Kurskoye Gorodishche. Outcrop of the Nadsnezha Beds at Lovat' River. Middle Frasnian. *Bothriolepis maxima* (Obruchev, 1947).

LUKA (23) Russia, Novgorod region, Zaluch'ye district, Luka village. Outcrop of clays, sand, sandstones of the Nadsnezha Beds at the middle current of Lovat' River. Middle Frasnian. *Bothriolepis maxima* (Obruchev, 1947).

BILOVO (24) Russia, Novgorod region, Cholm district. Exposure at the right bank of Malyi Tuder, tributary of Kun'ya River, near Bilovo hamlet. Lower Famennian. *Bothriolepis heckeri* sp.nov.

SOLODKA (25) Russia, Novgorod region. Outcrop containing a light globular sandstone at the right bank of Msta River in between Solodka and Navolok villages. Famennian. *Bothriolepis* sp.

LYUBITINO (26) Russia, Novgorod region, approximately 15 km N from Lyubitino town. Exposures of the deposits of the Upper Famennian and Lower Carboniferous L'nyanka Beds at the banks of Priksha, tributary of Belaya River. Upper Famennian. *Bothriolepis ornata* (Eichwald, 1860).

ZARUBINO (27) Russia, Novgorod region, approximately 25 km S-E from Lyubitino town. Quarry and mines not far from Zarubino village. Famennian. *Bothriolepis sp.*

PALUITSA (28) Russia, Leningrad region, Tikhvin district, S-E from Shugozero village. Exposures along the banks of Lower Paluitsa and Upper Paluitsa Rivers consisting of sandstones, clays, sands and siltstones of the Snezha and Prilovat' regional Substages. Upper Frasnian. *Bothriolepis maxima* (Ivanov, Khozatsky, 1986).

MONTSEVO (29) Russia, Leningrad region, Volkhov district. Outcrops at the right bank of Syass River along Montsevo village. Snetnaya Gora Beds of the Lower Frasnian. *Bothriolepis panderi* (Lahusen, 1880).

STOLBOVO (30) Russia, Leningrad region, Volkhov district. Exposure of variegated deposits of the Dubnik Beds at the right bank of Syas' River near Stolbovo village. Lower Frasnian. *Bothriolepis trautscholdi*.

VACHUKINTSY (31) Russia, Leningrad region. Exposure at Oyat' River not far from Vachukintsi village. Snetnaya Gora Beds of the Lower Frasnian. *Bothriolepis* sp.

Abbreviations used in text and figures

ADL anterior dorso-lateral plate
AMD anterior madian dorsal plate
AVL anterior ventro-lateral plate
a antero-lateral angle of AMD
ac rostral angle of head-shield
$ad_{1,2}$ anterior and posterior articular processes on Sm
alc antero-lateral angle of head-shield
alr postlevator thickenings of AMD
a_1Sm anterior attachment area for Sm
a_2Sm posterior attachment area for Sm
a.un unornamented area beneath fossa articularis pectoralis
Cd_1 dorsal central plate 1
Cd_2 dorsal central plate 2
Cd_3 dorsal central plate 3
Cd_4 dorsal central plate 4
Cd_5 dorsal central plate 5
Cv_1 ventral central plate 1
Cv_2 ventral central plate 2
Cv_3 ventral central plate 3
Cv_4 ventral central plate 4
c.al antero-lateral corner of subcephalic division of ventral lamina of AVL
cf.ADL area overlapping ADL
cf.AMD area overlapping AMD
cf.MxL area overlapping MxL
cf.PVL area overlapping PVL
cir semicircular pit-line groove
cit_1 crista transversalis interna anterior
cit_2 transverse thickening on the visceral surface of AVL
cri infra-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
crs supra-articular crista of ADL
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
$d.end_2$ external opening of canal for endolymphatic duct
$dlg_{1,2}$ 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
f.ap fossa articularis pectoralis
f.art articular fossa of ADL
f.ax axillary foramen of AVL
fe.orb orbital fenestra
fe.sorb suborbital 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
ifc_1 principal section of infraorbital sensory line on head-shield
ifc_2 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
Ml_2 lateral marginal plate 2
Ml_3 lateral marginal plate 3
Ml_4 lateral marginal plate 4
Ml_5 lateral marginal plate 5
Mm_1 mesial marginal plate 1
Mm_2 mesial marginal plate 2
Mm_3 mesial marginal plate 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
n.la lateral notch on Sm;
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
otr oblique transverse ridge of AMD
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
p lateral pit of head-shield
pa posterior corner of PMD
pbr processus brachialis
pc postero-lateral corner of Nu
pcl postero-lateral corner of AMD
pe pars pedalis of processus brachialis
pip pineal pit
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
prd preorbital depression
prh preorbital recess of head-shield
prnl postero-lateral process of Nu
pro processus obstans of trunk armour
pr.po antero-lateral corner of otico-occipital depression
pr.pl external postlevator process of AMD
prv_1 anterior ventral process of dorsal wall of trunk armour
prv_2 posterior ventral process of dorsal wall of trunk armour
pt_1 anterior ventral pit of dorsal wall of trunk armour
pt_2 posterior ventral pit of dorsal wall of trunk armour
Ro rostral plate
$Sclr_{1,2}$ plates 1 and 2 of sclerotic ring
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
sp area without ornamentation along the posterior margin of Pi
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

Table 1 of Supplement. Number of measured specimens of bothriolepid taxa, used in statistical analysis

Species	obr	cel	tra	eva	max	cur	jan	orn	cie	tub
Plates										
Head shield	-	6	-	8	-	9	-	-	5	-
Prm	14	9	11	8	6	9	-	-	8	-
La	11	7	14	8	5	9	-	5	13	-
Nu	7	10	18	10	9	9	5	7	22	7
Pn	8	7	11	9	5	9	-	5	12	6
AMD	17	8	19	11	16	6	6	9	21	5
PMD	23	8	24	11	6	-	5	9	12	10
ADL	9	-	12	7	9	-	-	-	14	-
MxL	8	-	11	7	5	8	7	5	30	-
AVL	-	-	14	5	6	7	-	-	13	-
PVL	5	-	7	5	7	5	-	-	25	-
Cd_1	12	5	-	5	-	-	-	-	18	-
Cv_1	7	-	8	-	5	5	-	-	9	-
Ml_2	-	-	5	7	-	6	5	-	9	-
At whole	121	36*	196*	16*	70*	44*	28	36*	179*	28

Abbreviations: obr - *Bothriolepis obrutschewi*; cel - *B.cellulosa*; tra - *B.trautscholdi*; eva - *B.evaldi*; max - *B.maxima*; cur - *B.curonica*; jan - *B.jani*; orn - *B.ornata*; cie - *B.ciecere*; tub - *Grossilepis tuberculata*

* Some specimens contain more than one plate

Table 2 of Supplement. The list of the measurements and indices

(1) Length of head shield (LHs): midline length of head shield excluding obtected nuchal area.

(2) Width of head shield (WHs): distance between posterolateral corners.

(3) Length of praemedian plate (LPrm).

(4) Rostral width of praemedian plate (WrPrm): length of rostral margin of praemedian.

(5) Orbital width of praemedian plate (WoPrm): length of orbital margin of praemedian.

(6) Width of orbital fenestra (WOf): greatest transverse width of orbital fenestra.

(7) Length of nuchal plate (LNu): distance from anterolateral corner to obtected area.

(8) Width of nuchal plate (WNu): width of nuchal plate across lateral corners.

(9) Length of trunk armour (LTs): distance from anterior extremity of AMD and posterior corner of PMD.

(10) Width of trunk armour (WTs): distance between lateral extremities of suture between ADL and MxL.

(11) Length of AMD (LAMD): midline length of AMD.

(12) Width of AMD (WAMD): distance between lateral corners of AMD.

(13) Anterior width of AMD (WaAMD): distance between anterolateral corners of AMD.

(14) Posterior width of AMD (WpAMD): distance between posterolateral corners of AMD (excluding overlap area).

(15) Tergal length of AMD (LtAMD): distance from tergal angle to anterior midline extremity of AMD.

(16) Length of PMD (LPMD): midline length of PMD.

(17) Width of PMD (WPMD): distance between lateral corners of PMD.

(18) Anterior width of PMD (WaPMD): distance between anterolateral corners of PMD.

(19) Length of anterior division of AMD (LlAMD): distance between anterior margin of AMD and lateral corner along midline.

(20) Length of ADL (LADL): distance from postnuchal angle to posterior extrimity of ADL.

(21) Width of ADL (WADL): distance between lateral margin and line, which is parallel to it, crossing the mesial extrimity of postnuchal angle.

(22) Posterior width of ADL (WpADL): length of posterior margin of dorsal lamina of ADL.

(23) Length of MxL (LMxL): distance between anteromesial and posterior corners, measured parallel to lateral margin of MxL.

(24) Width of MxL (WMxL): distance from distal corner to lateral margin of MxL.

(25) Anterior width of MxL (WaMxL): length of anterior margin of dorsal lamina of MxL.

(26) Height of MxL (HMxL): length of anterior margin of lateral lamina of MxL.

(27) Length of AVL (LAVL): distance between anterior and posterior extremities of AVL, measured parallel to mesial margin.

(28) Width of AVL (WAVL): distance from lateral margin to mesial extremities of AVL.

(29) Length of PVL (LPVL): distance between anterior and posterior extremities of PVL, measured parallel to mesial margin.

(30) Width of PVL (WPVL): distance from lateral margin to mesial extremities of PVL.

Continuation of table 2 of Supplement

(31-36) Length and width of Cd_1, Cv_1 and Ml_2, respectively.

(37) Length of lateral plate (LLa): distance from anteromesial to posterior corner of lateral plate.

(38) Width of lateral plate (WLa): distance from lateral corner of lateral plate to anterolateral corner of nuchal plate.

(39) Length of orbital margin of nuchal plate (TNu): distance between antero-lateral corners of nuchal plate.

(40) Length of anterior division off nuchal plate (SNu): distance from antero-lateral and lateral corners of nuchal plate, measured parallel to longitudinal axis of plate.

(41) Length of paranuchal plate (LPn): distance between anterior and posterior extremities of paranuchal plate, measured parallel to midline of head shield.

(42) Width of paranuchal plate (WPn): distance between lateral and mesial extremities of paranuchal plate, measured at right angle to midline of head shield.

(43) Mesial width of paranuchal plate (WmPn): distance from mesial extremity of paranuchal plate to lateral extremity of sensory line canal.

Indices, used in statistical analysis: WHs/LHs, LHs/LPrm, LPrm/WrPrm, WrPrm/WoPrm, LNu/WNu, LNu/SNu, WNu/TNu, WOf/WHs, LLa/WLa, LPn/WPn, WPn/WmPn, LAMD/WAMD, LtAMD/LAMD, LlAMD/LAMD, WAMD/WaAMD, WAMD/WpAMD, LPMD/WPMD, WaPMD/WPMD, LADL/WADL, LADL/WpADL, LMxL/WMxL, LMxL/HMxL, WMxL/WaMxL, LAVL/WAVL, LPVL/WPVL, LCd_1/WCd_1, LCv_1/WCv_1, LMl_2/WMl_2.

Table 3 of Supplement. The results of regression analysis of selected variable pairs in several species of *Bothriolepis*

Variables (x/y)	a	Sa	ts	df(N-2)	Signif. level
		B.trautscholdi			
LPrm/WrPrm	0.900	0.081	1.240	9	NS
WrPrm/WoPrm	0.753	0.139	1.778	9	NS
LNu/WNu	0.888	0.044	2.572	16	*
LAMD/WAMD	0.998	0.014	0.152	17	NS
LtAMD/LAMD	1.256	0.040	6.394	17	***
WaAMD/WpAMD	0.954	0.020	2.277	17	*
LPMD/WPMD	0.993	0.012	0.595	21	NS
WaPMD/WPMD	1.229	0.022	10.222	21	***
		B.evaldi			
LPrm/WrPrm	0.592	0.077	5.269	6	***
WrPrm/WoPrm	0.410	0.097	6.055	6	***
LNu/WNu	0.846	0.058	2.630	8	*
WOf/WHs	0.906	0.114	0.823	6	NS
LHs/LPrm	1.525	0.078	6.773	6	***
LAMD/WAMD	1.306	0.096	3.202	8	*
LtAMD/LAMD	0.947	0.103	0.516	8	NS
WaAMD/WpAMD	0.694	0.113	2.712	8	*
LPMD/WPMD	1.036	0.100	0.359	8	NS
WaPMD/WPMD	0.816	0.031	5.966	8	***
		B.maxima			
LPrm/WrPrm	0.704	0.214	1.382	3	NS
WrPrm/WoPrm	0.906	0.015	0.586	3	NS
LNu/WNu	0.856	0.114	1.262	5	NS
WOf/WHs	1.414	1.304	0.318	1	NS
LHs/LPrm	0.989	0.051	0.217	1	NS
LAMD/WAMD	0.983	0.113	0.153	13	NS
LtAMD/LAMD	0.851	0.065	2.285	13	*
WaAMD/WpAMD	0.606	0.153	2.566	13	*
LPMD/WPMD	1.284	0.145	1.958	4	NS
WaPMD/WPMD	0.834	0.150	1.107	4	NS

		B.curonica			
LPrm/WrPrm	0.636	0.237	1.532	9	NS
WrPrm/WoPrm	0.960	0.446	0.090	9	NS
LNu/WNu	0.940	0.089	0.665	12	NS
WOf/WHs	0.929	0.339	0.209	7	NS
LHs/LPrm	1.923	0.609	1.515	7	NS
		B.jani			
LAMD/WAMD	0.828	0.078	2.193	4	NS
LtAMD/LAMD	1.093	0.063	1.473	4	NS
WaAMD/WpAMD	0.645	0.198	1.796	4	NS
LPMD/WPMD	1.028	0.098	0.288	2	NS
WaPMD/WPMD	1.006	0.136	0.047	2	NS
		B.ornata			
LPrm/WrPrm	0.852	0.056	2.657	1	NS
WrPrm/WoPrm	1.214	0.024	8.789	1	NS
LNu/WNu	0.866	0.083	1.614	7	NS
LAMD/WAMD	1.022	0.045	0.486	7	NS
LtAMD/LAMD	1.049	0.076	0.647	7	NS
WaAMD/WpAMD	1.413	0.291	1.419	7	NS
LPMD/WPMD	1.095	0.030	3.152	7	*
WaPMD/WPMD	0.885	0.055	2.090	7	NS
		B.ciecere			
LPrm/WrPrm	0.819	0.141	1.288	8	NS
WrPrm/WoPrm	0.804	0.130	1.507	8	NS
LNu/WNu	0.732	0.071	3.798	16	***
WOf/WHs	1.088	0.552	0.160	3	NS
LHs/LPrm	0.491	0.272	1.874	3	NS
LAMD/WAMD	1.032	0.068	0.474	16	NS
LtAMD/LAMD	1.012	0.071	0.169	16	NS
WaAMD/WpAMD	0.946	0.107	0.503	16	NS
LPMD/WPMD	0.936	0.044	1.455	11	NS
WaPMD/WPMD	0.874	0.054	2.335	11	*

Abbreviations of the significance levels: *** - 0.1%; ** - 1%; * - 5%; NS - not significant

Table 4 of Supplement. Variability of the proportions of the head shield in several *Bothriolepis* species

Variables / Species	WHs/LHs	LHs/LPrm	WO/WHs	d_{Hs}
B.ciecere	7.96	4.85	6.86	6.56
B.curonica	5.71	5.01	5.83	5.52
B.evaldi	7.99	12.03	6.70	8.91
B.cellulosa	5.38	8.84	3.65	5.96
On the average	6.76	7.68	5.76	

Table 5 of Supplement. Variability of the Prm plate in several *Bothriolepis* species

Variables / Species	LPrm/WrPrm	WrPrm/WoPrm	d_{Prm}
B.ciecere	8.85	3.77	6.31
B.curonica	7.21	10.63	8.92
B.maxima	5.81	8.65	7.23
B.evaldi	15.81	10.76	13.29
B.trautscholdi	6.78	10.76	8.77
B.cellulosa	9.60	14.60	12.10
B.obrutschewi	8.39	10.05	9.22
On the average	8.92	9.89	

Table 6 of Supplement. Variability of the Nu plate in several bothriolepid species

Variables / Species	LNu/WNu	LNu/SNu	WNu/TNu	d_{Nu}
B.ciecere	2.24	3.76	5.58	3.86
B.ornata	11.42	14.23	10.97	12.21
B.jani	5.11	5.17	5.16	5.15
B.curonica	4.06	10.46	7.34	7.29
B.maxima	6.61	11.28	7.03	8.31
B.evaldi	7.49	13.88	4.27	8.55
B.trautscholdi	7.46	7.33	6.68	7.16
B.cellulosa	6.32	9.27	9.07	8.22
B.obrutschewi	8.97	7.59	9.69	8.75
G.tuberculata	6.86	7.34	8.89	7.70
On the average	6.65	9.22	7.47	

Table 7 of Supplement. Variability of the Pn plate in several bothriolepid species

Variables / Species	LPn/WPn	WPn/WmPn	d_{Pn}
B.ciecere	8.34	4.26	6.30
B.ornata	10.84	2.12	6.48
B.curonica	11.79	4.63	8.21
B.maxima	8.62	4.41	6.52
B.evaldi	6.80	7.59	7.20
B.trautscholdi	11.82	9.76	10.79
B.cellulosa	16.09	7.57	11.83
B.obrutschewi	10.92	5.79	8.36
G.tuberculata	9.49	5.53	7.51
On the average	10.52	5.74	

Table 8 of Supplement. Variability of the AMD in several bothriolepid species

Variables / Species	1	2	3	4	5
B.ciecere	8.12	6.98	7.34	10.90	7.34
B.ornata	4.17	6.71	4.12	17.03	9.51
B.jani	8.68	5.48	10.14	14.60	12.33
B.curonica	8.69	6.45	4.36	11.85	9.13
B.maxima	7.28	4.92	6.43	12.46	8.59
B.evaldi	8.90	6.77	8.04	10.74	10.76
B.trautscholdi	6.14	6.57	5.96	6.41	7.06
B.cellulosa	4.94	5.17	4.17	18.63	10.79
B.obrutschewi	2.34	6.46	3.55	7.03	5.81
G.tuberculata	10.00	12.09	12.05	11.64	8.27
On the average	6.93	6.76	6.62	12.13	8.96

Variables: 1 - LAMD/WAMD; 2 - LtAMD/LAMD; 3 - LlAMD/LAMD; 4 - WAMD/WaAMD; 5 - WAMD/WpAMD

Table 9 of Supplement. Variability of the PMD in several bothriolepid species

Variables / Species	LPMD/WPMD	WaPMD/WPMD	d_{PMD}
B.ciecere	5.14	7.83	6.49
B.ornata	5.65	10.54	8.10
B.jani	4.24	14.39	9.32
B.maxima	6.70	7.06	6.88
B.evaldi	9.67	9.80	9.74
B.trautscholdi	9.06	9.58	9.32
B.cellulosa	12.73	8.65	10.69
B.obrutschewi	7.15	4.98	6.07
G.tuberculata	7.92	5.79	6.86
On the average	7.58	8.74	

Table 10 of Supplement. Variability of the ADL in several *Bothriolepis* species

Variables / Species	LADL/WADL	LADL/WpADL	d_{ADL}
B.ciecere	9.24	9.28	9.26
B.maxima	11.10	11.87	11.49
B.evaldi	8.62	9.10	8.86
B.trautscholdi	10.13	10.13	10.13
B.obrutschewi	9.37	11.11	10.24
On the average	9.69	10.30	

Table 11 of Supplement. Variability of the MxL in several *Bothriolepis* species

Variables / Species	LMxL/WMxL	LMxL/HMxL	WMxL/WaMxL
B.ciecere	4.85	8.98	7.88
B.ornata	5.26		13.78
B.jani	4.56	10.34	7.81
B.curonica	4.58	4.77	9.33
B.maxima	3.47		17.52
B.evaldi	6.98		9.99
B.trautscholdi	3.69		8.95
B.obrutschewi	6.90	9.09	9.12
On the average	5.04	8.30	10.55

Table 12 of Supplement. Variability of the AVL and PVL in several *Bothriolepis* species

Variables / Species	LAVL/WAVL	LPVL/WPVL
B.ciecere	12.79	7.45
B.curonica	10.98	6.88
B.maxima	6.73	8.41
B.evaldi	10.19	8.73
B.trautscholdi	8.51	9.07
B.obrutschewi		10.36
On the average	9.84	8.48

Table 13 of Supplement. Variability of the pectoral fin plates in several *Bothriolepis* species

Variables / Species	LCd_1/WCd_1	LCv_1/WCv_1	LMl_2/WMl_2
B.ciecere	5.73	4.58	7.12
B.jani			12.43
B.curonica		7.01	13.97
B.maxima		7.89	
B.evaldi	7.53		13.82
B.trautscholdi		9.32	9.44
B.cellulosa	9.23		
B.obrutschewi	5.12	7.88	
On the average	6.90	7.34	11.36

Distribution of vertebrates in the Upper Devonian of the Main Devonian Field

	?	Frasnian														Famennian							
			Plavinas				Daugava																
	Gauja	Amata	Snetnaya Gora Beds	Pskov Beds	Chudovo Beds	Dubnik	Porkhov Beds	Svinord Beds	Il'men' Beds	Buregi Beds	Altovo Beds	Snezha	Pamūšis	Stipinai	Amula	Eleja	Joniškis	Kursa	Akmene	Mūri	Švēte	Žagare	Ketleri
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ganosteus stellatus Rohon	+																						
Psammolepis paradoxa Ag.	+																						
P. alata Mark-Kurik	+																						
P. heteraster Gross	+																						
P. venyukovi Obr.	+	+																					
Psammosteus sp. A	+																						
Asterolepis ornata Eichw.	+																						
Plourdosteus livonicus (Eastm.)	+	+																					
Devononchus concinnus Gross	+	+																					
Haplacanthus ehrmanensis Gross	+																						
Lodeacanthus gaujicus Upeniece	+																						
Nostolepis sp.	+																						
Glyptolepis baltica Gross	+	+																					
Laccognathus panderi Gross	+	+																					
Latvius sp.	+																						
Panderichthys rhombolepis (Gross)	+	+																					
Coelacanthiformes gen.et sp.nov.	+																						
Crossipterus crassus Gross	+																						
Psammolepis undulata Ag.	+	+																					
Cheirolepis sp.	+																						
Psammosteus maeandrinus Ag.		+	+	+																			
P. livonicus Obr.		+																					
P. praecursor Obr.		+	+																				
P. cuneatus Obr.		+																					
P. levis Obr.		+																					
Asterolepis radiata Rohon		+	+	+																			
Bothriolepis prima Gross		+																					
B. obrutschewi Gross		+																					
Holoptychius cf. *nobilissimus* Ag.		+	+	+		+	+	+	+		+	+	+		+	+	+	+	+	+	+	+	+
Eusthenopteron obruchevi Vorob.		+																					
Struniiformes gen.indet.		+	+	+												+	+	+	+	+	+		+
Dipteridae gen.indet.		+	+	+																			
Psammosteus asper Obr.		+	+																				
Karelosteus weberi Obr.		+	+																				
Ctenurella pskovensis (Obr.)			+																				
Rhamphodopsis sp.			+																				
"*Ptyctodus*" sp.			+	+	+	+	+	+	+	+	+												
Rhynchodus sp.			+	+	+	+			+														
Plourdosteus mironovi (Obr.)			+	+																			
Grossilepis tuberculata (Gross)			+	+	+																		
Bothriolepis cellulosa (Pand.)			+	+																			
Bothriolepis panderi Lahusen			+																				
Haplacanthus perseensis Gross			+	+																			
Glyptolepis sp.			+																				
Laccognathus sp.			+																				
Latvius grewingki (Gross)			+	+																			

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Eusthenopteron saevesoederberghi Jarvik																							
Strunius rolandi (Gross)																							
Rhinodipterus secans (Gross)																							
Griphognathus minutidens Gross																							
Moythomasia perforata (Gross)																							
Ptyctodontidae gen.indet.																							
Conchodus jerofejewi (Pander)																							
Platycephalichthys rohoni Vorob.																							
Psammosteus megalopteryx (Traut.)																							
Psammosteus pectinatus Obr.																							
Holonema radiatum Obr.												?											
Gyroplacosteus panderi Obr.																							
Plourdosteus trautscholdi (Eastm.)																							
Asterolepis syasiensis Lyarskaya																							
Bothriolepis trautscholdi Jaekel																							
Eastmanosteus egloni (O.Obr.)																							
Jarvikina wenjukowi (Rohon)																							
Parapanderichthys stolbovi Vorob.																							
"Dipterus" verneuili Pander																							
Coccosteidae gen.indet.																							
Eusthenopteron sp.																							
Psammosteus falcatus Obr.																							
P.tenuis Obr.																							
Aspidosteus heckeri Obr.																							
Plourdosteus sp.																							
Bothriolepis maxima Gross																							
Platycephalichthys bischoffi Vorob.																							
Devononchus laevis (Gross)																							
Asterolepis? amulensis Lyarsk.																							
Bothriolepis evaldi Lyarsk.																							
Grossilepis spinosa (Gross)																							
Taeniolepis speciosa Gross																							
Antiarcha gen.indet.																							
Obruchevichthys gracilis Vorob.																							
Eusthenodon sp.																							
"Dipterus" cf.*marginalis* Ag.																							
Bothriolepis sp.																							
Dipnoi gen.indet.																							
Bothriolepis curonica Gross																							
Devononchus sp.																							
Haplacanthus sp.																							
Panderichthys sp.																							
Dipnoi gen.indet.																							
Palaeoniscidae gen.indet.																							
Dinichthyidae gen.indet.																							
Phyllolepis sp.																							
Bothriolepis sp.																							
Protacrodus sp.																							
Glyptolepis? dellei (Gross)																							
Chelyophorus sp.																							
Megapomus heckeri Vorob.																							
Osteolepididae gen.indet.																							
B.jani Lukševičs																							
Homacanthus sveteensis Gross																							
Stethacanthidae gen.indet.																							
Phyllolepis tolli Vasiliauskas																							
Bothriolepis ornata Eichw.																							

	17	18	19	20	21	22	23	24
Devononchus tenuispinus (Gross)								
Platycephalichthys skuenicus Vorob.								
Cryptolepis sp.								
Conchodus sp.								
Bothriolepis sp.								
Bothriolepis ciecere Lyarsk.								
Devononchus ketleriensis Gross								
Ventalepis ketleriensis Schultze								
Cryptolepis grossi Vorob.								
Eusthenopteridae gen. indet.								
Glyptopomus? bystrowi (Gross)								
Orlovichthys cf. *limnatis* Krupina								
Ventastega curonica Ahlberg, Lukševičs & Lebedev								
Tetrapoda gen. indet.								

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Explanation of plates

Plate 1

Figs.A-E. *Bothriolepis prima* Gross.

A, incomplete head-shield LGI 5-2202, x1.5.

B, incomplete head-shield LGI 5-2203, x1.5.

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 view (produced by V.Talimaa), x1.2.

Daugava River near Pastamuiža, Latvia.

Fig.F. *Bothriolepis panderi* Lahusen, lectotype, the complete head-shield and anterior part of the trunk armour MM 1/96, x1.

Montsevo locality at Syas' River, Russia.

Plate 2

Figs.A-E. *Bothriolepis obrutschewi* Gross.

A, head-shield and AMD plate, probably belonged to the same individual LGI 5-2345, x1.

B, head-shield of small individual LGI 5-2255, x2.

C-E, restored 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 view (produced by V.Talimaa), x1.

Daugava River near Pastamuiža, Latvia.

Plate 3

Figs.A-I. *Bothriolepis trautscholdi* Jaekel.

A, B, head-shield PIN 330/117 in dorsal and visceral view, x1.

C, D, head-shield PIN 330/113 in dorsal and visceral view, x1.

E, head-shield PIN 330/125 in dorsal view, x1.

F, Prm plate PIN 330/46 in dorsal view, x1.

G, Prm plate PIN 330/126 in dorsal view, x1.

H, Prm plate PIN 330/127 in dorsal view, x1.

A-H, Stolbovo locality at Syas' River, Russia.

Plate 4

Figs.A-B. *Bothriolepis* sp.

A, B, La plate PIN 2665/1 in dorsal and visceral view, x1.

Figs.C-N. *Bothriolepis trautscholdi* Jaekel.

C, La plate PIN 330/124 in dorsal view, x1.

D, La plate PIN 330/115 in visceral view, x1.

E, La plate PIN 330/112 in dorsal view, x1.

F, Pn plate LP 14/4 in dorsal view, x1.

G, Pn plate LDM 63/138 in dorsal view, x2.

H, Nu plate LDM 63/149 in dorsal view, x1.

I, J, Nu and Pp plates PIN 330/42 in dorsal and visceral view, x1.

K, Sm plate PIN 330/116 in lateral view, x1.

L, M, Sm plate PIN 330/114 in lateral and visceral view, x1.

N, proximal segment of the pectoral fin PIN 330/68 in ventral view, x1.

A, B, Vachukintsy locality at Oyat' River, Russia.

C-N, Stolbovo locality at Syas' River, Russia.

Plate 5

Figs.A-M *Bothriolepis trautscholdi* Jaekel.

A, AMD plate LDM 63/18 in dorsal view, x1.
B, AMD plate LDM 63/24 in dorsal view, x1.
C, AMD plate LDM 63/46 in dorsal view, x1.
D, AMD plate LDM 63/41 in dorsal view, x1.
E, AMD plate LDM 63/57 in visceral view, x1.
F, AMD plate LDM 63/44 in visceral view, x1.
G, AMD plate LDM 63/13 in visceral view, x1.
H, AMD plate PIN 330/55 in dorsal view, x1.
I, AMD plate PIN 330/56 in dorsal view, x1.
J, AMD plate PIN 330/52 in dorsal view, x1.
K, AMD plate LDM 63/37 in dorsal view, x1.
L, AMD plate PIN 330/53 in dorsal view, x1.
M, AMD plate LDM 63/8 in dorsal view, x1.
Stolbovo locality at Syas' River, Russia.

Plate 6

Figs.A-J. *Bothriolepis trautscholdi* Jaekel.

A, PMD plate PIN 330/47 in dorsal view, x1.
B, PMD plate PIN 330/50 in visceral view, x1.
C, PMD plate PIN 330/48 in dorsal view, x1.
D, MxL plate PIN 330/99 in dorsal view, x1.
E, ADL plate LDM 63/98 in dorsal view, x1.
F, ADL plate PIN 330/86 in dorsal view, x1.
G, H, ADL plate PIN 330/87 in dorsal and lateral view, x1.
I, J, ADL plate PIN 330/98 in dorsal and anterior view, x1.
Stolbovo locality at Syas' River, Russia.

Figs.K-M. *Bothriolepis heckeri* sp.nov.

K, holotype, AMD plate PIN 835/42 in dorsal view, x1.
L, incomplete AMD plate PIN 835/41 in dorsal view, x1.
M, incomplete La, Pn and Pmg plates PIN 835/40 in dorsal view, x1.
Malyy Tuder River not far from Bilovo village, Russia.

Plate 7

Figs.A-J. *Bothriolepis evaldi* Lyarskaja.

A, holotype, articulated head, trunk and pectoral fin armour LDM 67/86 in dorsal view, x2.
B, details of the head-shield of the holotype, x3.
C, details of the head-shield of specimen LDM 67/39 in dorsal view, x3.
D, head-shield LDM 280/1 in dorsal view, x1.
E, articulated head and trunk armour LDM 67/14 in dorsal view, x1.
F, somewhat flattened and deformed articulated head, trunk and left pectoral fin armour LDM 67/13 in ventral view, x1.
G, articulated head, trunk, left pectoral fin armour and right Cv_1 LDM 67/3 in ventral view, x1.
H, head and trunk armour in visceral view with articulated right pectoral fin in ventral view LDM 67/6, x1.
I, articulated trunk armour LDM 67/2 in dorsal view, x1.
J, articulated trunk armour LDM 67/10 in dorsal view, x2.
A-C, E-J, Kalnamuiža 1 locality at Amula River, Latvia.
D, Kaibala River not far from Lielvārde, Latvia.

Plate 8

Figs. A-E. *Bothriolepis curonica* Gross.

A, holotype, head-shield LDM 15/32, x1.
B, head-shield LDM 98/10, x1.
C, head-shield LDM 89/1, x1.
D, head-shield LDM 98/86, x1.
E, PMD plate LDM 98/36, x1.
A, Bienes locality at Imula River, Latvia.
B-E, locality at Amula River upstream Kalnamuiža watermill, Latvia.

Plate 9

Figs. A-C. *Bothriolepis curonica* Gross.

A, AMD plate LDM 15/121, x1.
Bienes locality at Imula River, Latvia.
B, AMD plate LDM 98/21, x1.
C, ADL plate LDM 98/58, x1.
Amula River upstream Kalnamuiža watermill.

Plate 10

Figs. A-G. *Bothriolepis curonica* Gross.

A, ADL plate LDM 98/94, x1.
B, ADL plate LDM 89/12, x1.
C, MxL plate LDM 89/2, x1.
D, MxL plate LDM 98/54, x1.2.
E, AVL plate LDM 98/30, x1.
F, AVL plate LDM 89/7, x1.
G, distal segment of the pectoral fin LDM 89/4, x1.
Amula River upstream Kalnamuiža watermill.

Plate 11

Figs. A-F. *Bothriolepis curonica* Gross.

A, AVL plate in visceral view with articulated proximal segment of pectoral fin LDM 98/78, x1.
B, PVL plate LDM 98/45, x1.
C, PVL plate LDM 98/41, x1.
D, Ml_2 plate LDM 98/76, x1.
E, Cv_1 plate LDM 98/90, x1.
F, Cv_1 plate LDM 98/77, x1.
Amula River upstream Kalnamuiža watermill.

Plate 12

Figs. A-U. *Bothriolepis jani* Lukševičs.

A, Prm plate LDM 100/144, x2.
B, La plate LDM 100/369, x2.
C, Pp plate LDM 100/429, x2.
D, paratype, Nu plate LDM 100/142, x3.
E, Nu plate LDM 100/430, x2.
F, Nu plate LDM 100/141, x2.
G, Nu plate LDM 100/372, x2.
H,I, paratype, AMD plate LDM 100/67 in dorsal and visceral view, x2.
J, AMD plate LDM 100/431, x2.
K, PMD plate LDM 100/76, x2.
L, PMD plate LDM 100/83, x2.
M, ADL plate LDM 100/122, x2.
N, ADL plate LDM 100/121, x2.
O, holotype, MxL plate LDM 100/88, x2.
P,R, AVL plate LDM 100/98, in dorsal and visceral view, x1.
S, PVL plate LDM 100/434, x2.
T, proximal segment of the pectoral fin LDM 100/435, x2.
U, fragment of the Cv_1 plate LDM 100/131, x2.
Klūnas locality at Skujaine River.

Plate 13

Figs. A-M. *Bothriolepis ornata* Eichw.

A,B, head-shield LDM 100/31 in dorsal and visceral view, x1.
C, head-shield LDM 100/32in dorsal view, x1.
D,E, La plate LGI 5/2053 in dorsal and visceral view, x1.
F, La plate LDM 100/44, x1.
G, Nu plate LDM 100/399, x1.
H, Nu plate LDM 100/39, x1.
I, Nu plate LDM 100/38, x1.
J, Nu plate LDM 100/398, x1.
K,L, Nu plate LDM 100/42 in dorsal and visceral view, x1.
M, Pn plate LDM 100/402, x1.
Klūnas locality at Skujaine River.

Plate 14

Figs. A-E. *Bothriolepis ornata* Eichw.

A,B, AMD plate LDM 100/2 in dorsal and visceral view.
C,D, AMD plate LGI 5/2046 in dorsal and visceral view.
E, AMD plate LDM 100/8 in dorsal view.
Klūnas locality at Skujaine River.

Plate 15

Figs. A-H. *Bothriolepis ornata* Eichw.

A,B, AMD plate LDM 100/403 in dorsal and visceral view, x0.6.
C,D, AMD plate LDM 100/405 in dorsal and visceral view, x1.
E,F, AMD plate LDM 100/404 in dorsal view, x1.
G, AMD plate LGI 5/2099 in dorsal view, x1.
H, AMD plate LDM 100/406 in dorsal view, x1.
Klūnas locality at Skujaine River.

Plate 16

Figs.A-B. *Bothriolepis ornata* Eichw. AMD plate LDM 100/4, x1.
Klūnas locality at Skujaine River.

Plate 17

Figs.A-I. *Bothriolepis ornata* Eichw.
A,B, PMD plate LDM 100/357 in dorsal and visceral view, x1.
C,D, PMD plate LDM 100/355 in dorsal and visceral view, x1.
E,F, PMD plate LDM 100/356 in dorsal and visceral view, x1.
G,H, PMD plate LDM 100/354 in dorsal and visceral view, x1.
I, PMD plate LDM 100/13 in dorsal view, x1.
Klūnas locality at Skujaine River.

Plate 18

Figs.A-G. *Bothriolepis ornata* Eichw.
A,B, PMD plate LDM 100/408 in dorsal and visceral view, x0.5.
C,D, PMD plate LDM 100/409 in dorsal and visceral view, x0.5.
E, MxL plate LGI 5/2058, x1.
F, MxL plate LDM 100/21, x1.
G, MxL plate LDM 100/20, x1.
Klūnas locality at Skujaine River.

Plate 19

Figs.A-G. *Bothriolepis ornata* Eichw.
A, ADL plate LDM 100/16, x1.
B, ADL plate LDM 100/411, x0.5.
C, ADL plate LDM 100/412, x0.5.
D, PVL plate LDM 100/416, x1.
E, PVL plate LDM 100/27, x1.
F, G, AVL plate LDM 100/414 in ventral and visceral view, x0.5.
Klūnas locality at Skujaine River.

Plate 20

Figs.A-E. *Bothriolepis ornata* Eichw.
A, B, AVL plate LDM 100/24 in ventral and visceral view, x1.
C, AVL plate with articulated Cd_1 and Cv_1 plates LDM 100/523, x0.5.
D, processus brachialis LDM 100/365, x1.
E, MV plate LDM 100/30, x2.
Klūnas locality at Skujaine River.

Plate 21

Figs.A-F. *Bothriolepis ornata* Eichw.
A, anterior part of proximal segment of pectoral fin articulated with fragment of AVL plate LGI 5/2060, x1.
B, Cd_1 plate LDM 100/418, x1.
C, Cd_1 plate LDM 100/417, x0.5.
D, Cv_1 plate LDM 100/421, x1.
E, Cd_2 plate LDM 100/424, x1.
F, distal segment of pectoral fin LDM 100/45, x1.
Klūnas locality at Skujaine River.

Plate 22

Figs.A-V. *Bothriolepis ciecere* Lyarskaja.

A, head-shield LDM 81/101, x1.
B, head-shield LDM 81/545, x1.
C, D, Prm plate LDM 57/2 in dorsal and visceral view, x1.
E, F, La plate LGI 5/2034A in dorsal and visceral view, x1.
G, La plate LDM 81/600, x1.
H, I, Pi plate LDM 57/12 in dorsal and visceral view, x1.
J, Pi plate LDM 57/13, x1.
K, praelateral plate LDM 57/732, x1.
L, praelateral plate LDM 57/730, x1.
M, N, Nu plate LGI 5/2024 in dorsal and visceral view, x1.
O, Nu, Pn, fragmentary Pp, La plates LDM 43/337, x1.
P, R, Nu plate LGI 5/2025 in dorsal and visceral view, x1.
S, Nu plate LGI 2026, x1.
T, Nu plate LDM 57/18, x1.
U, V, Pn plate LDM 57/721, x1.
A,B,G,O, Pavari locality at Ciecere River;
C-F, H-N, P-V, Ketleri locality at Venta River.

Plate 23

Figs.A-J. *Bothriolepis ciecere* Lyarskaja.

A, holotype, AMD plate LDM 43/303 in dorsal view, x1.
B, AMD plate LDM 81/372 in dorsal view, x0.8.
C, AMD plate LDM 81/28 in dorsal view, x0.8.
D, E, AMD plate LGI 5/2020 in dorsal and visceral view, x1.
F, AMD plate LDM 43/5082 in dorsal view, x0.5.
G, H, AMD plate LGI 5/2046, in dorsal and visceral view, x0.6.
I, J, PMD plate LGI 5/2023 in visceral and dorsal view, x0.5.
A-C,F, Pavari locality at Ciecere River;
D,E,G-J, Ketleri locality at Venta River.

Figs.K,L. Bothriolepis sp.indet.2

Prm plate LP 14/7 in dorsal and visceral view, x1.
Zarubino, Novgorod region, Russia.

Plate 24

Figs.A-K. *Bothriolepis ciecere* Lyarskaja.

A,B, PMD plate LDM 57/722 in dorsal and visceral view, x1.
C, ADL plate LDM 43/5120, x1.
D, ADL plate LDM 43/306, x1.
E, ADL plate LDM 81/371, x1.
F, MxL plate LDM 81/193, x1.
G, MxL plate LDM 43/305, x1.
H, MxL plate 81/427, x1.
I, MxL plate LDM 81/423, x1.
J, MxL plate LDM 81/422, x1.
K, MxL plate LDM 81/424, x1.
C-K, Pavari locality at Ciecere River;
A,B, Ketleri locality at Venta River.

Plate 25

Figs. A-J. *Bothriolepis ciecere* Lyarskaja.

A, PVL plate LDM 81/445, x0.5.

B, PVL plate LDM 81/78, x1.

C, PVL plate LDM 81/444, x1.

D, PVL plate LDM 81/77, x1.

E, posterior part of the ventral lamina of PVL plate with characteristic ornament along the ventro-lateral ridge, LGI 5/2022, x1.

F, articulated AVL plates LDM 81/318 and 81/319, x1.

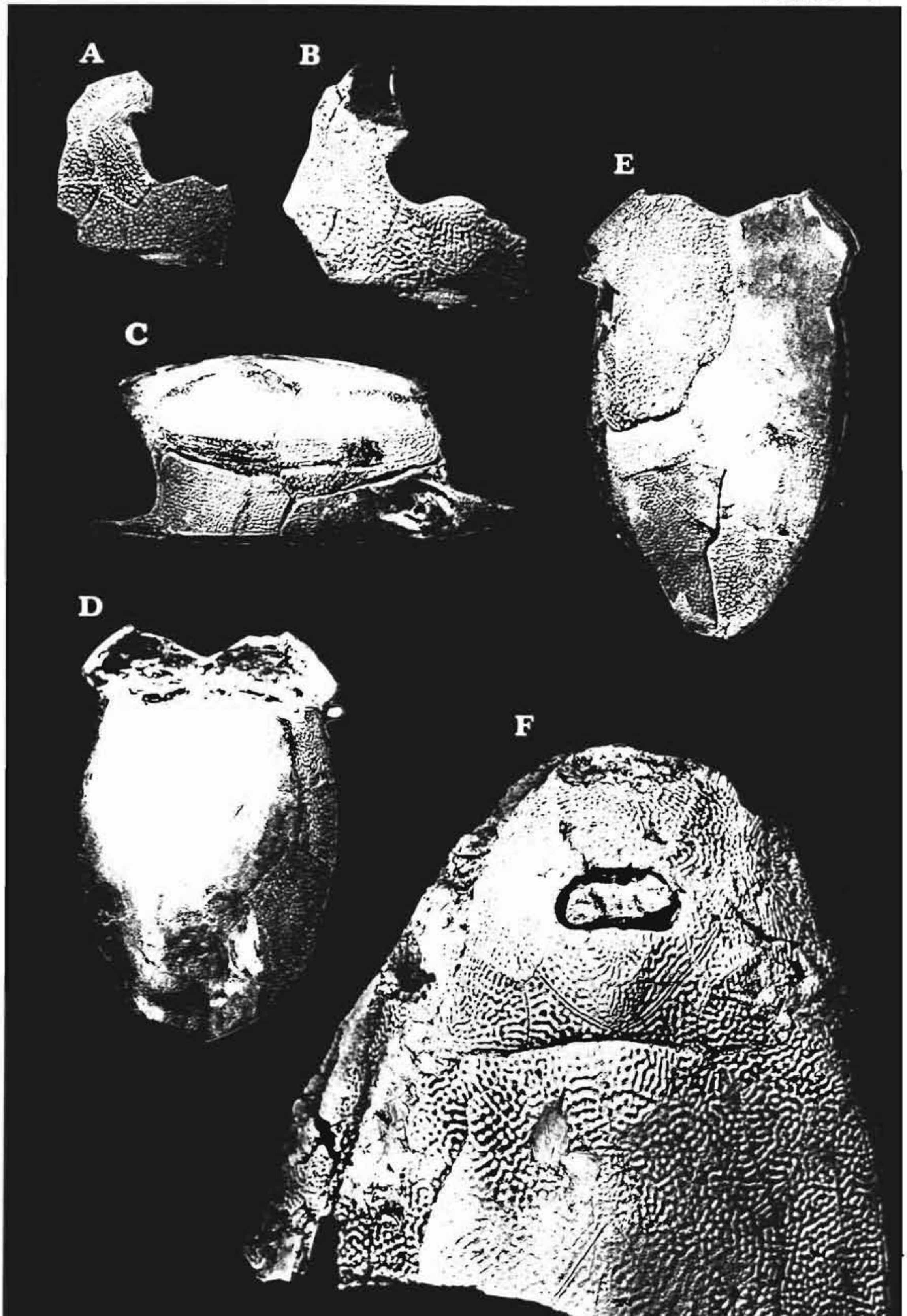
G, AVL plate in visceral view with articulated proximal segment of pectoral fin LDM 81/434, x1.

H, AVL plate in visceral view with articulated proximal segment of pectoral fin, Nu and Pp plates in dorsal view, LDM 81/435, x1.

I, J, AVL, incomplete ADL, Cd_1 and Cv_1 LDM 81/434, in ventral and lateral view, x0.5.

A-D, F-J, Pavāri locality at Ciecere River;

E, Ketleri locality at Venta River.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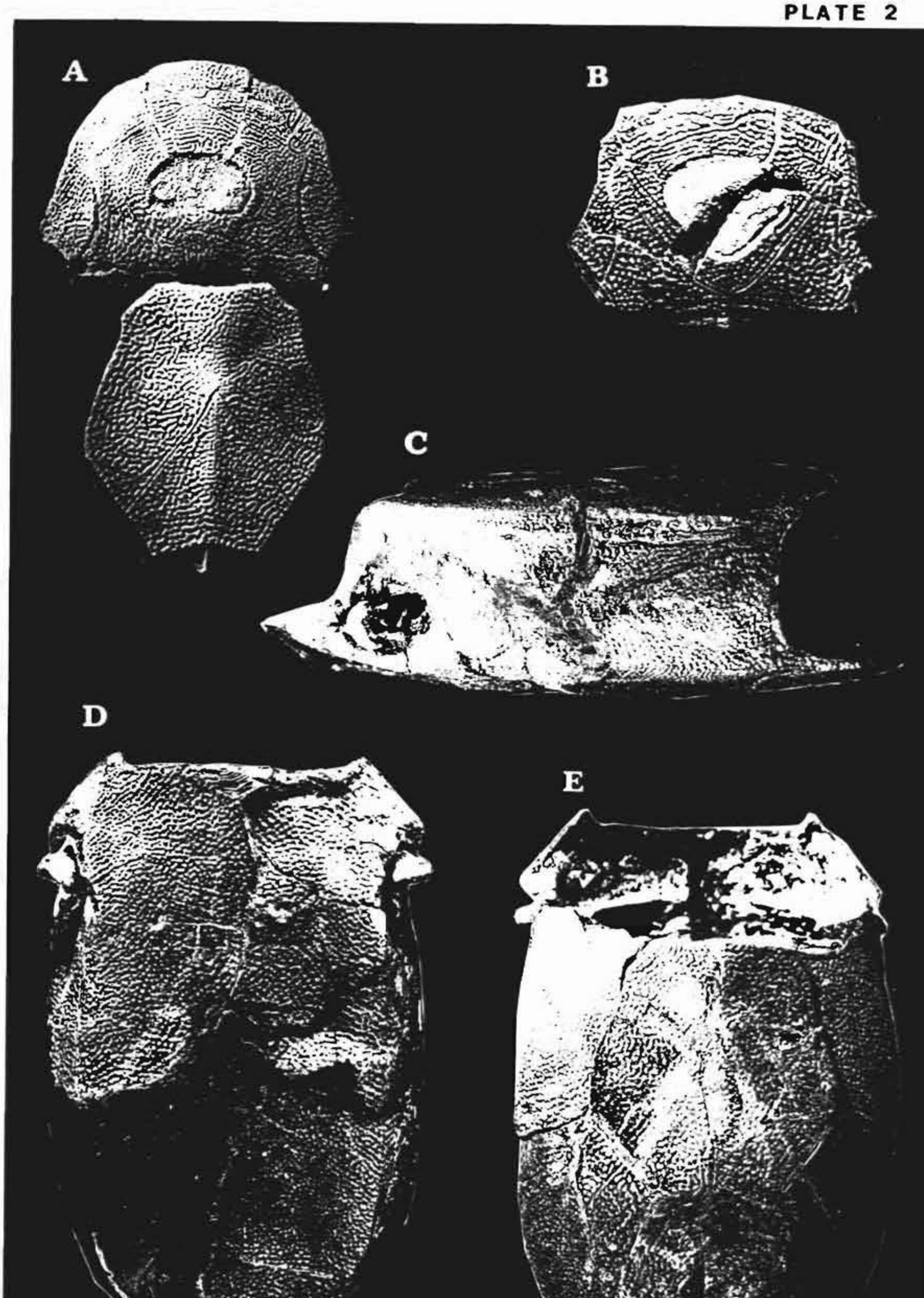
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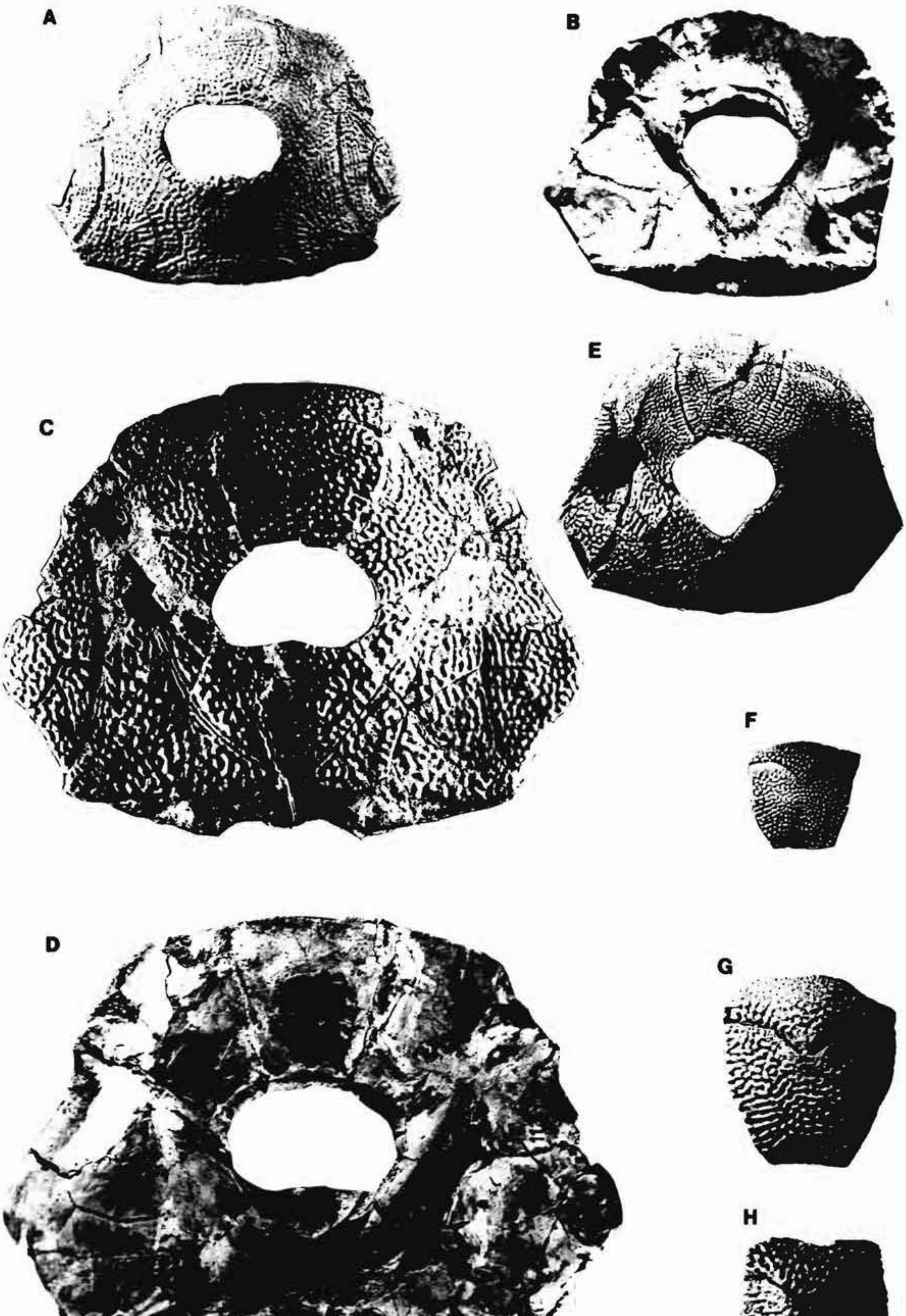
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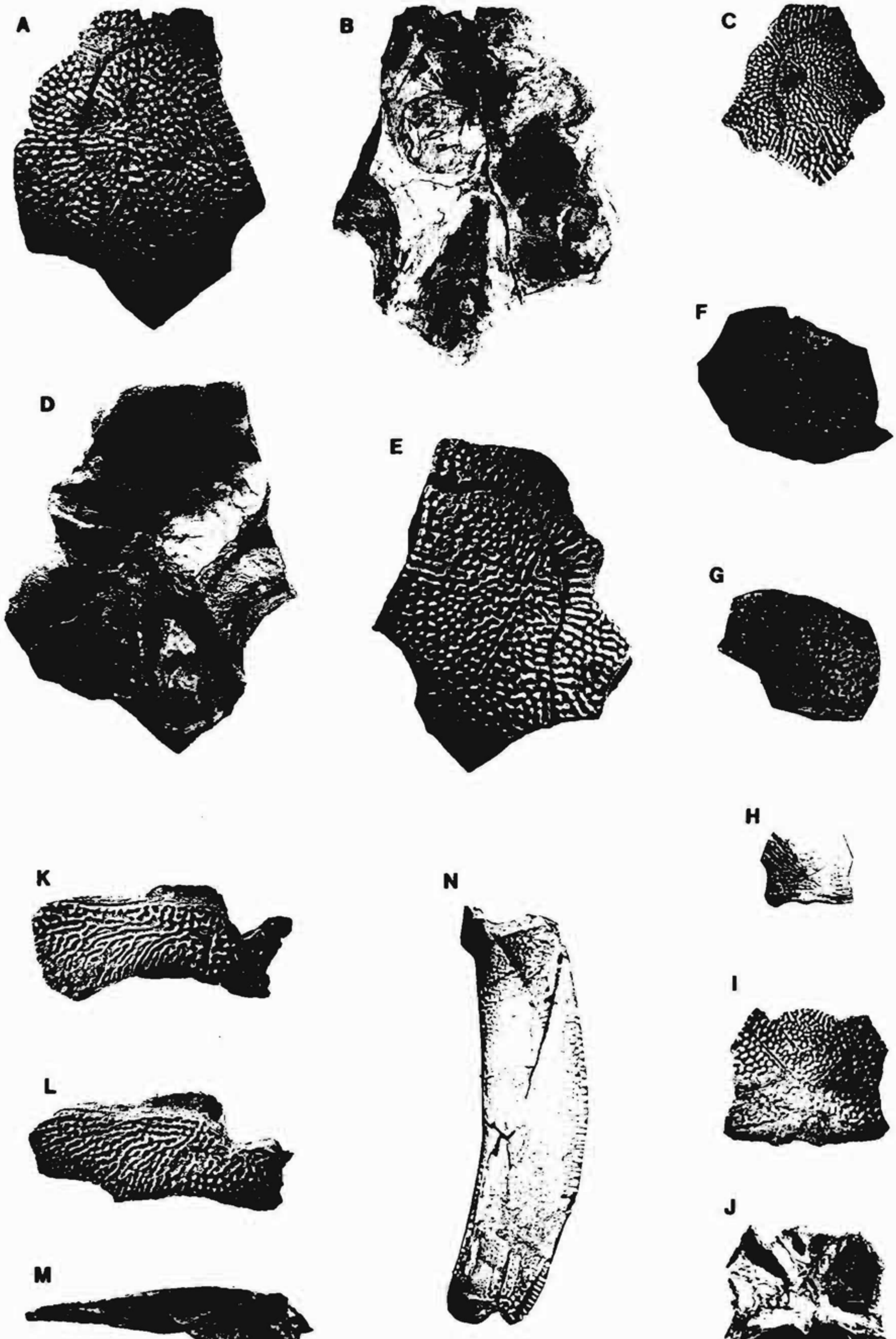

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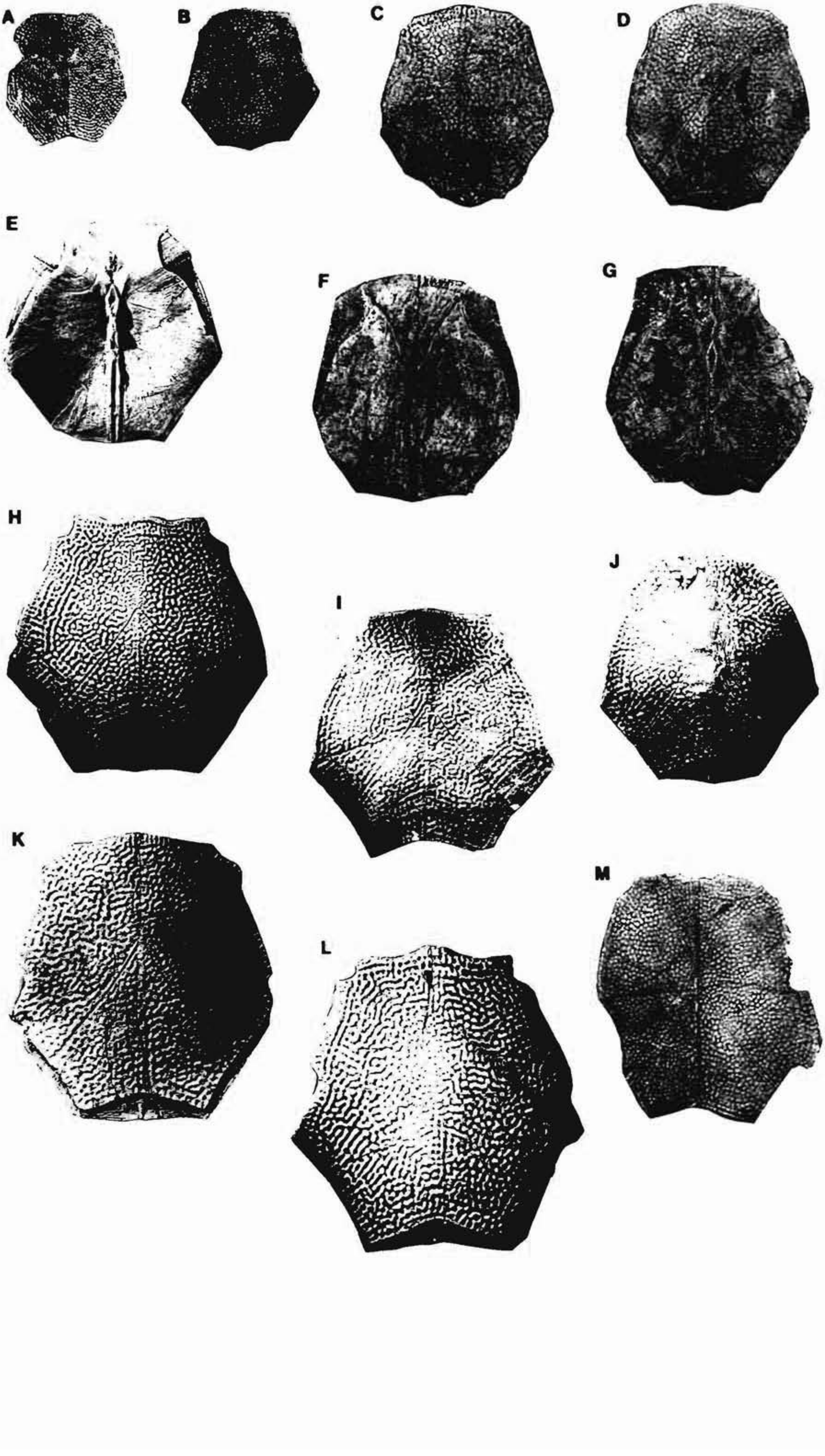

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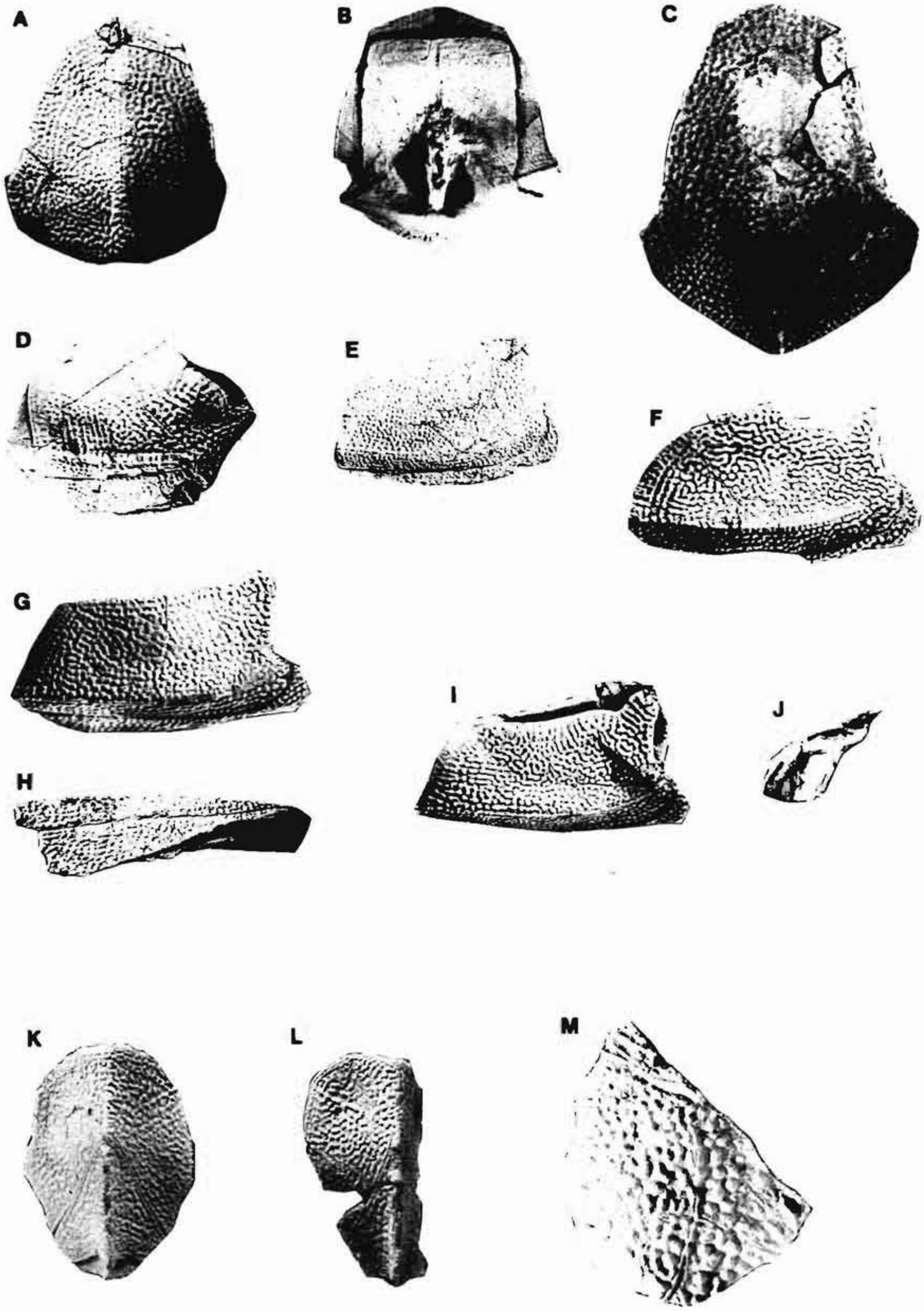

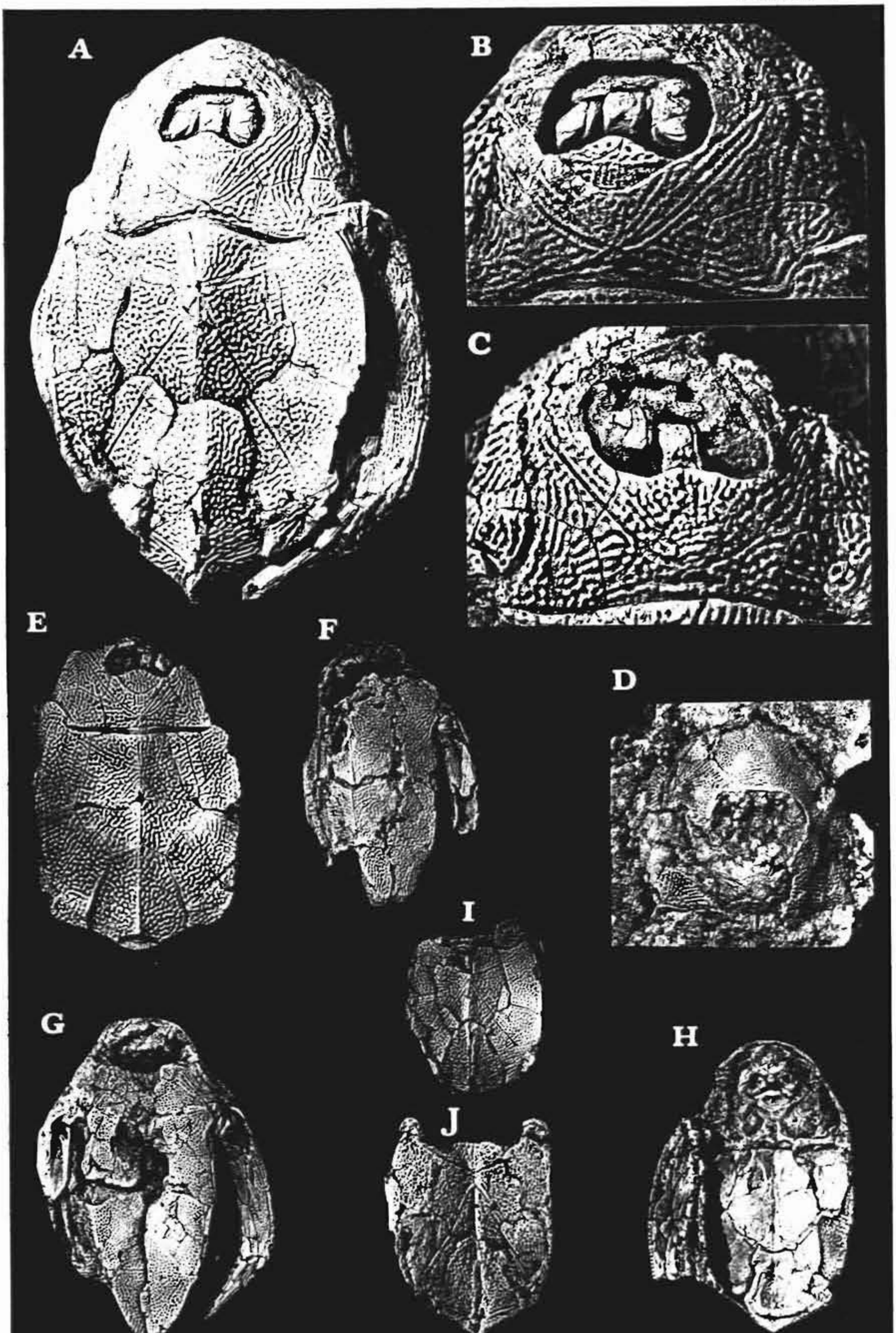
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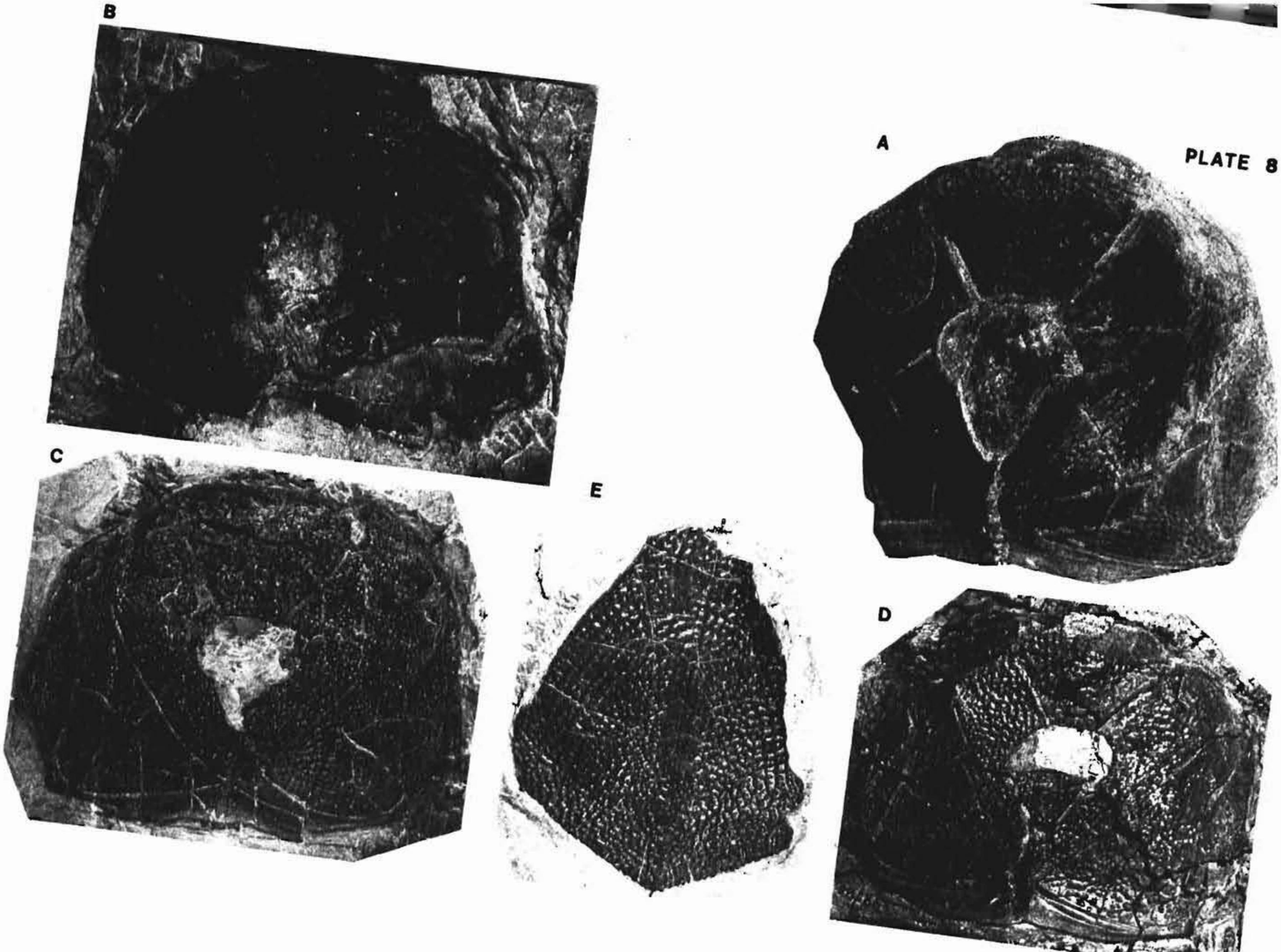
PLATE 8



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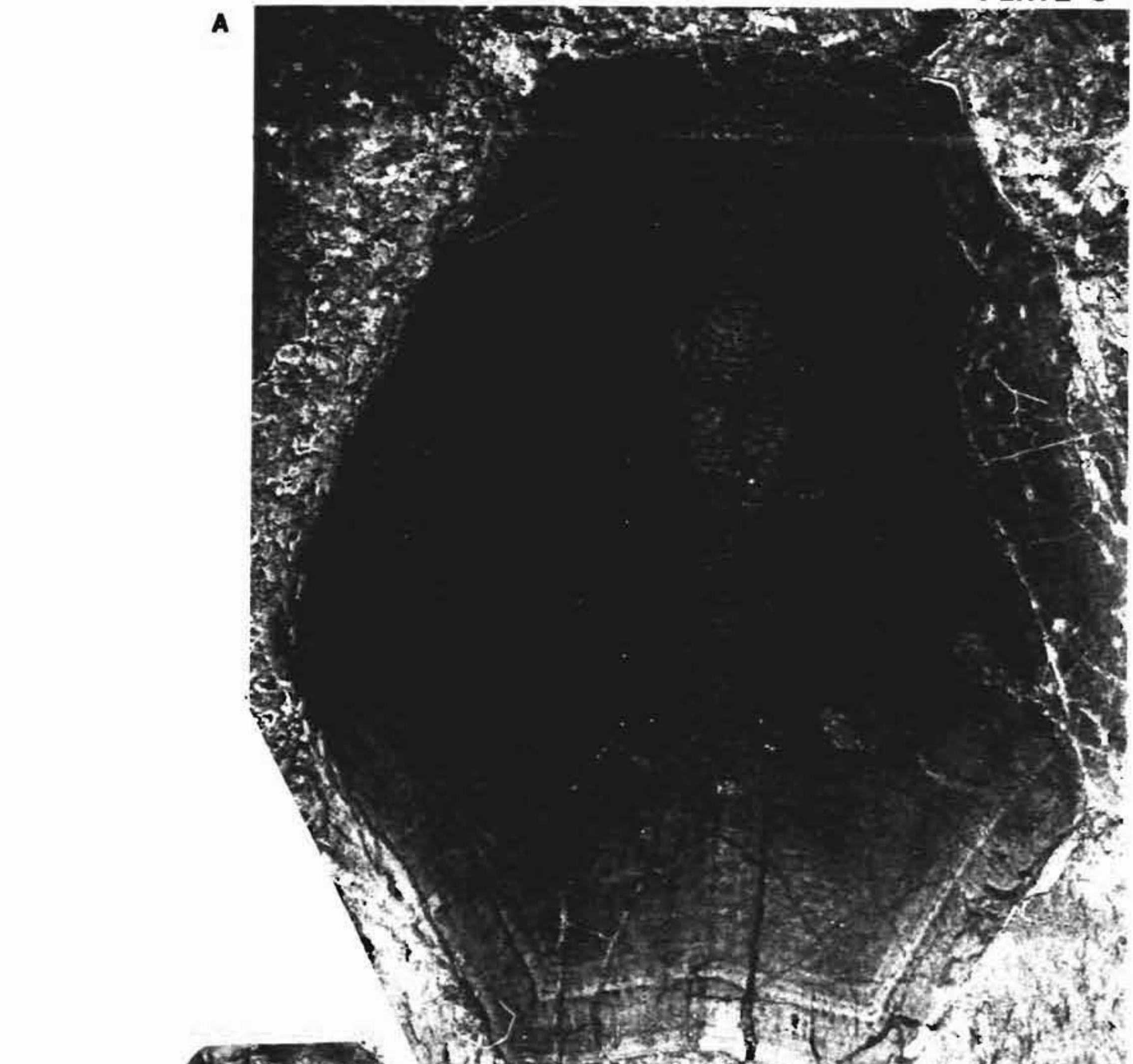

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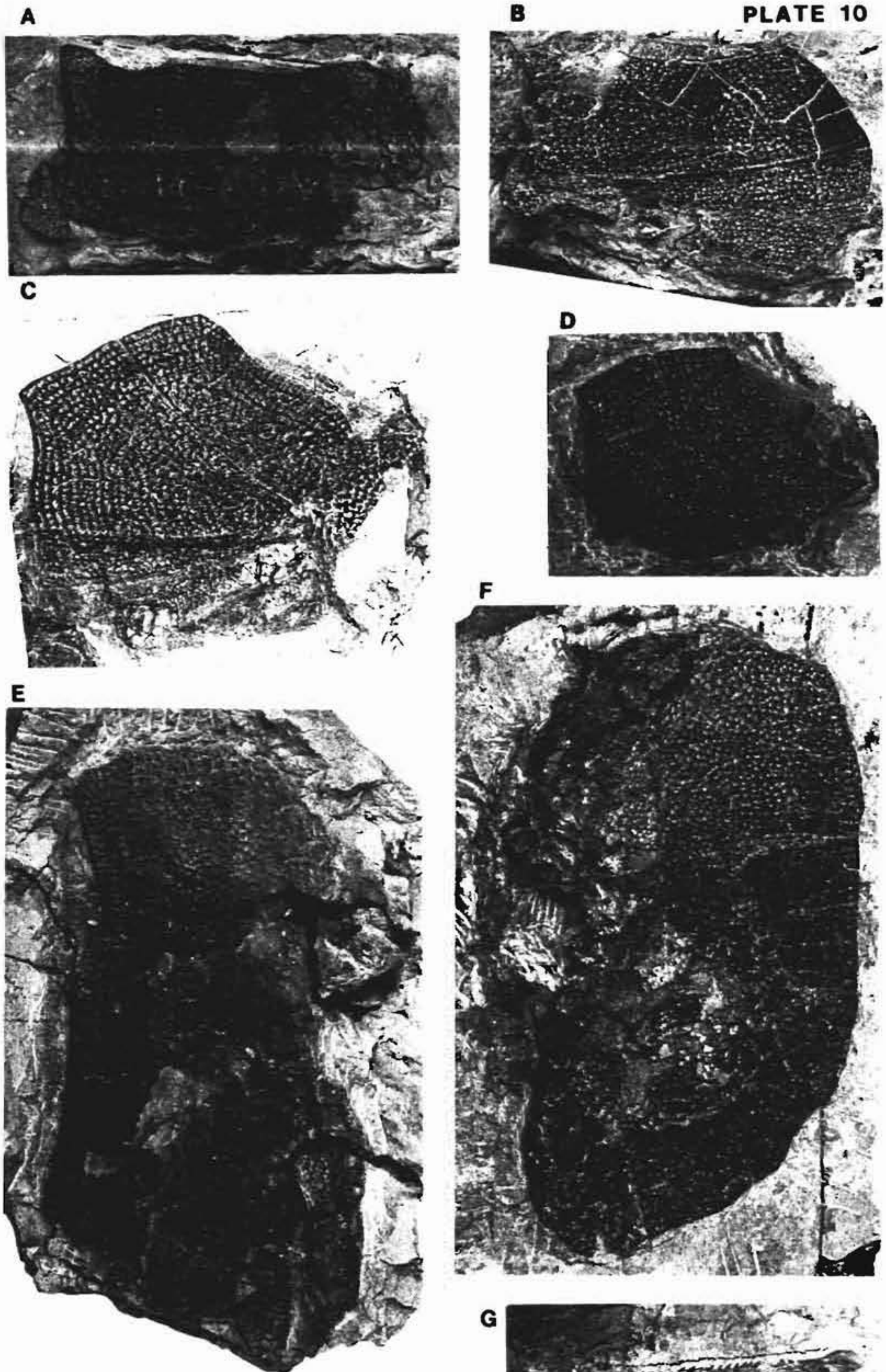

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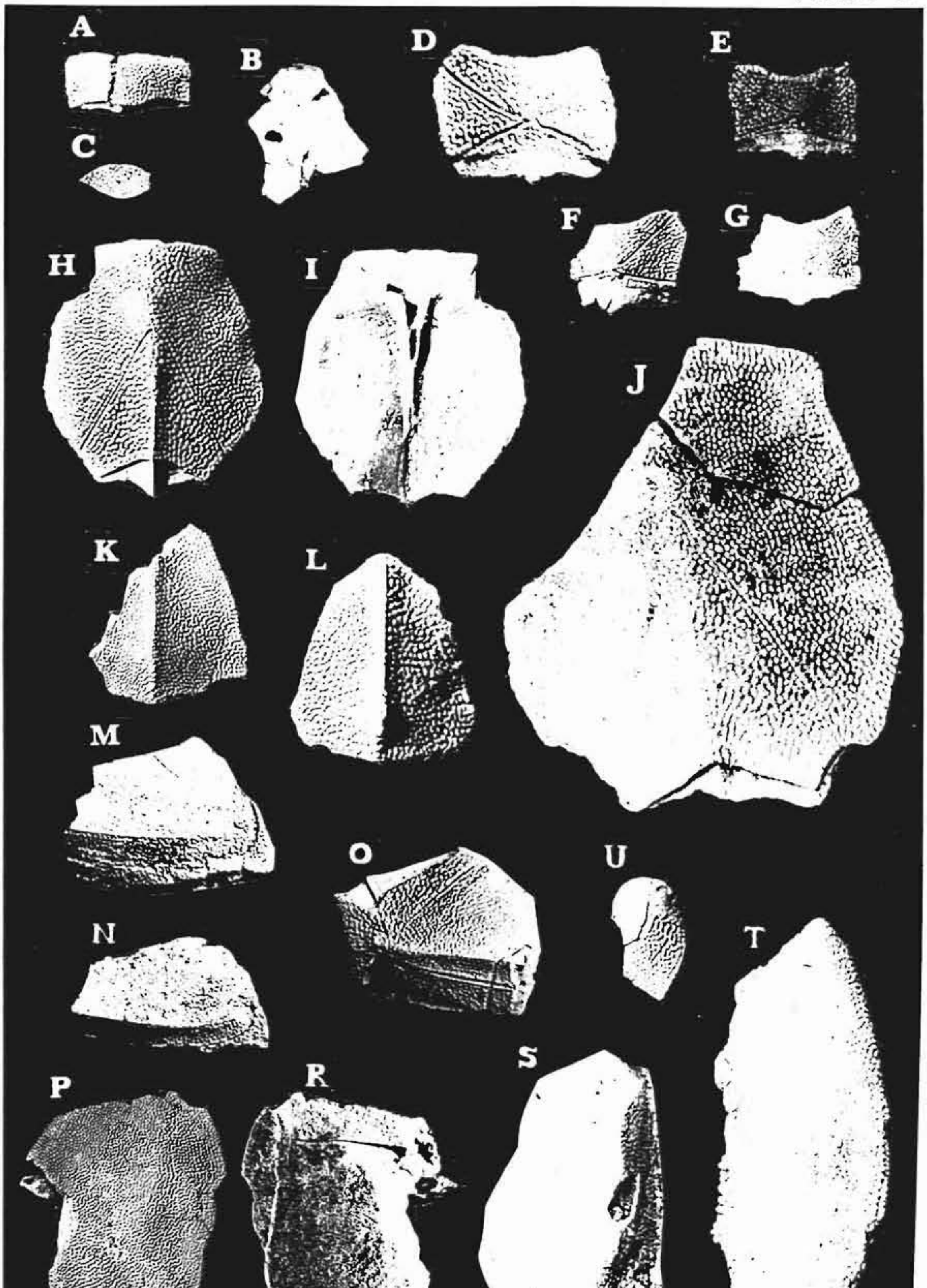
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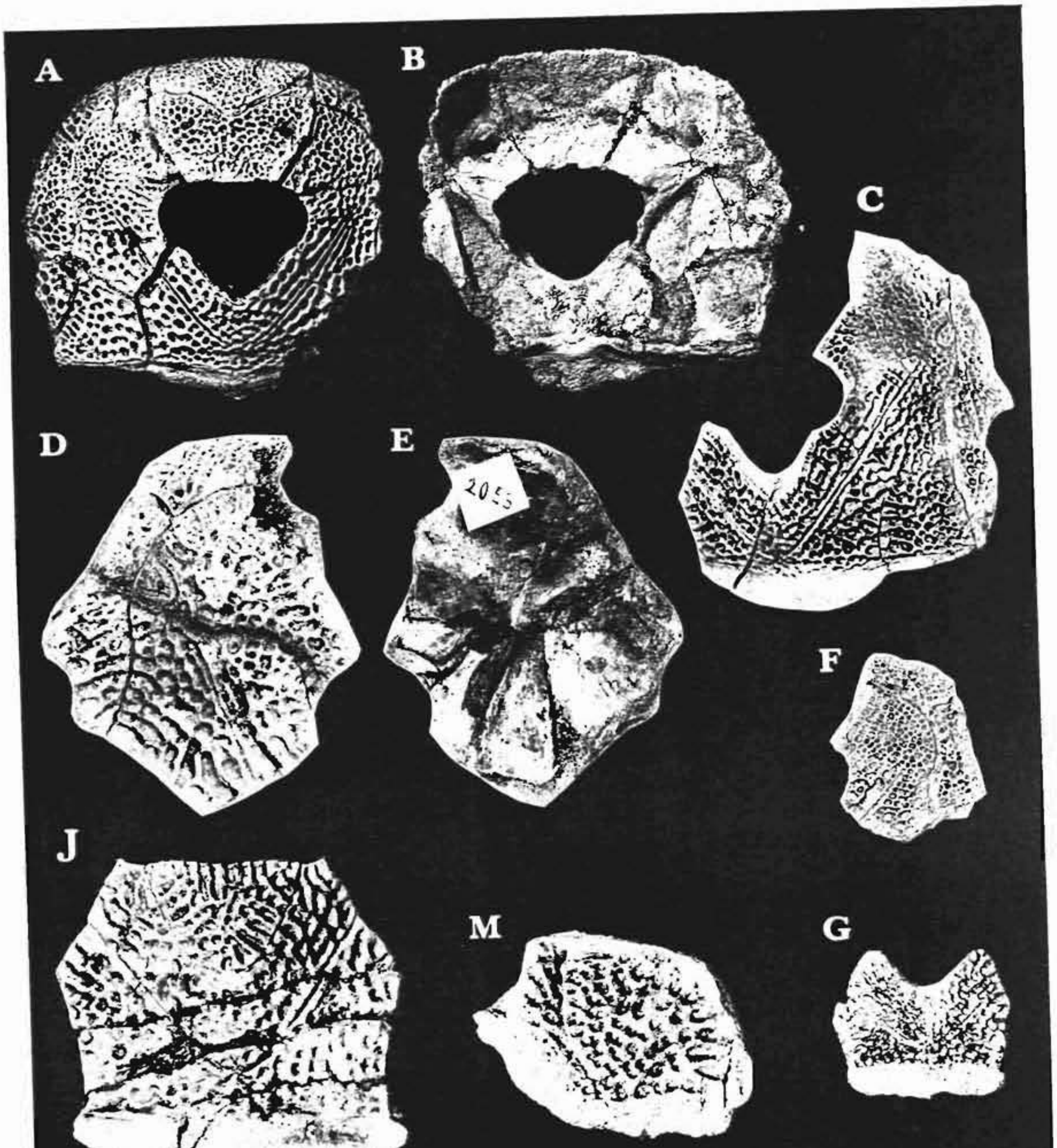
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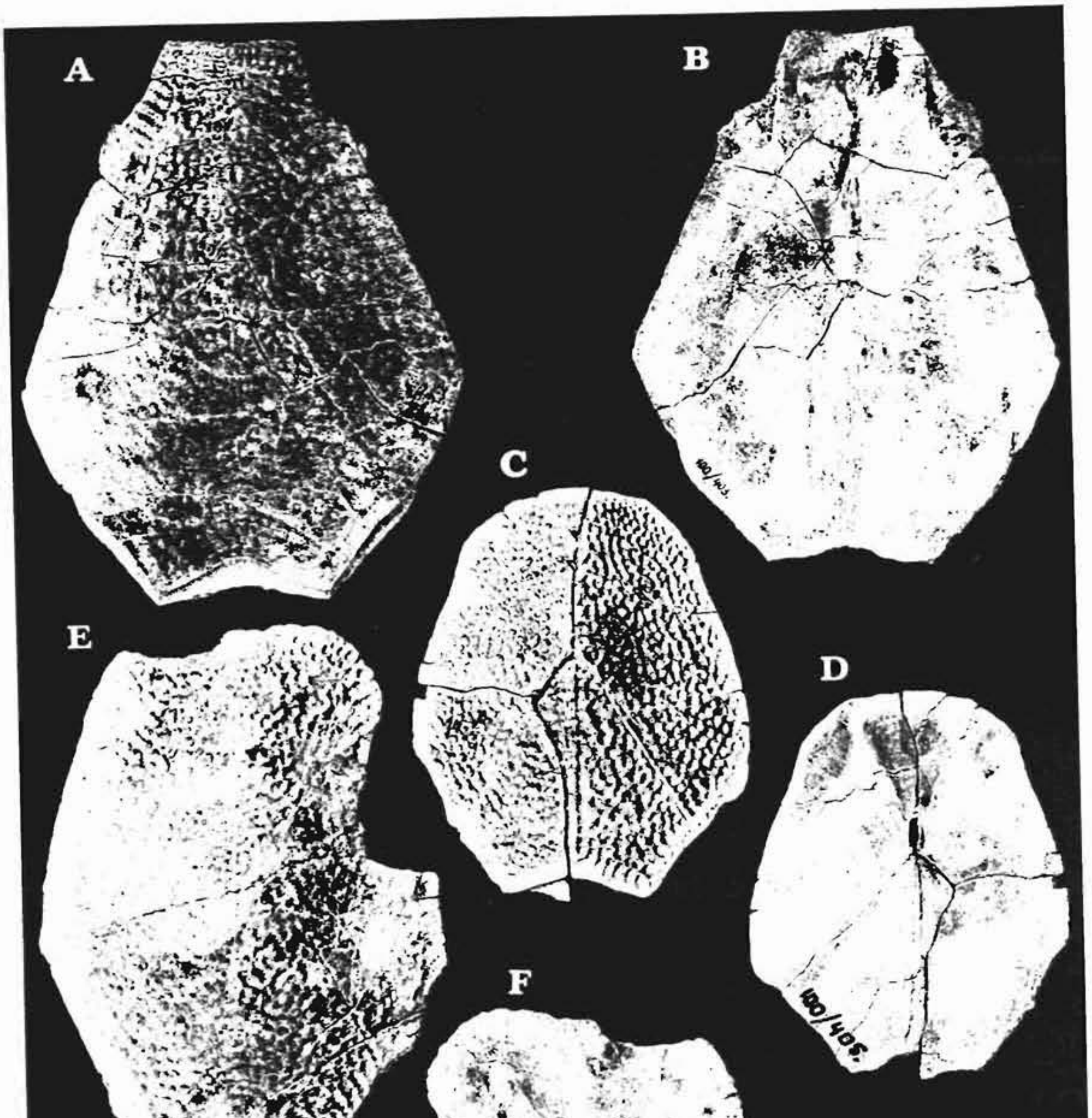
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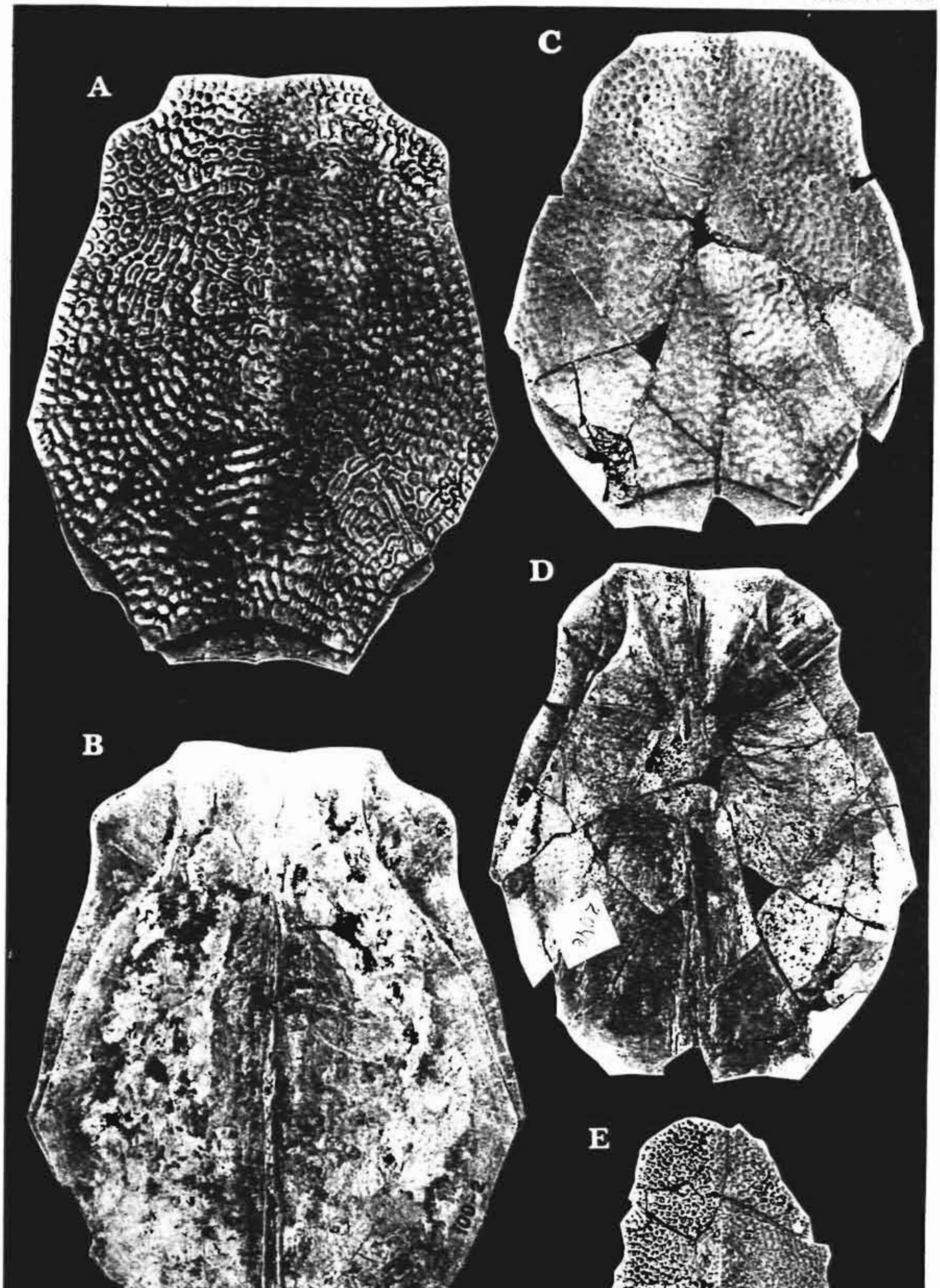
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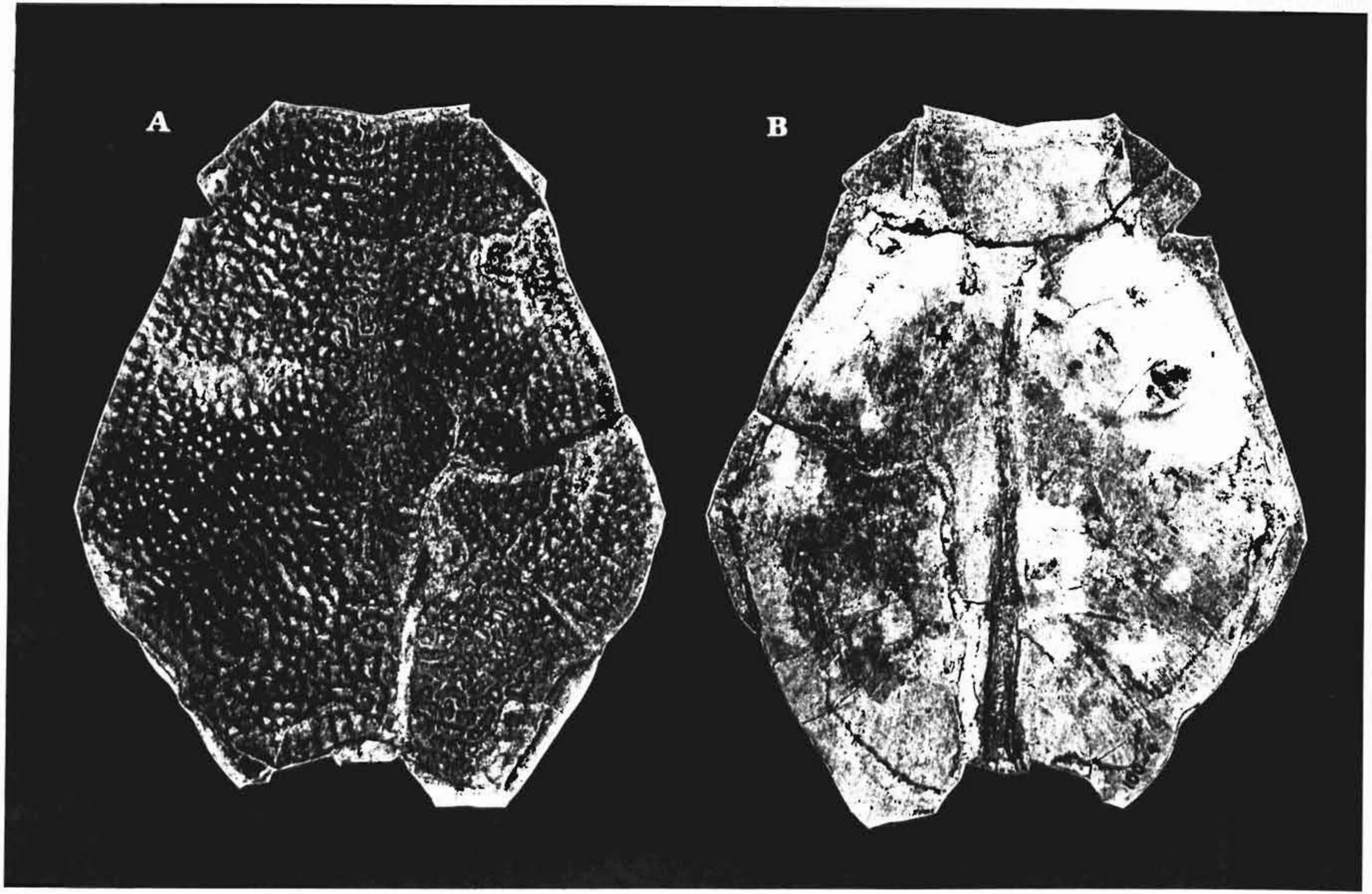

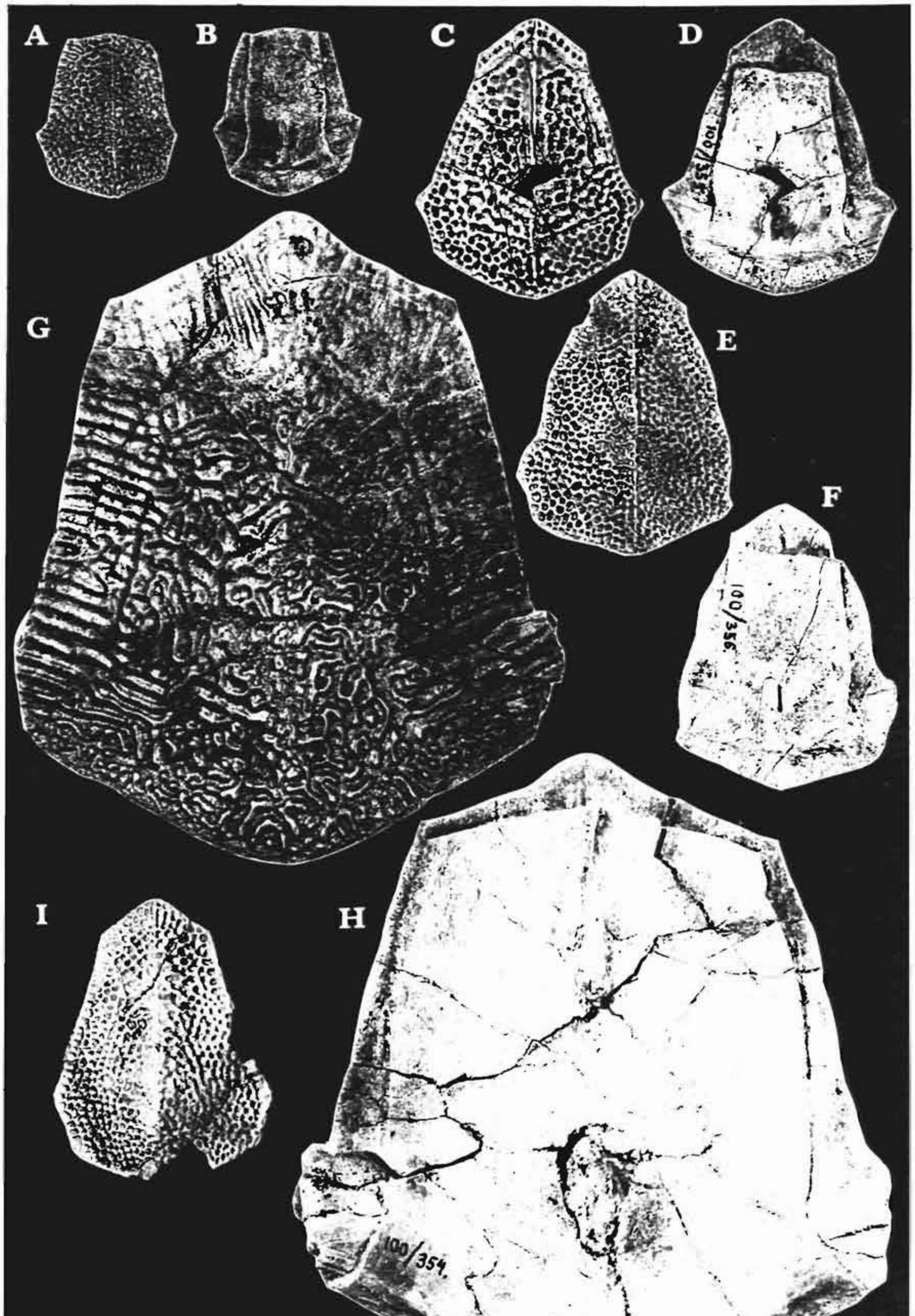
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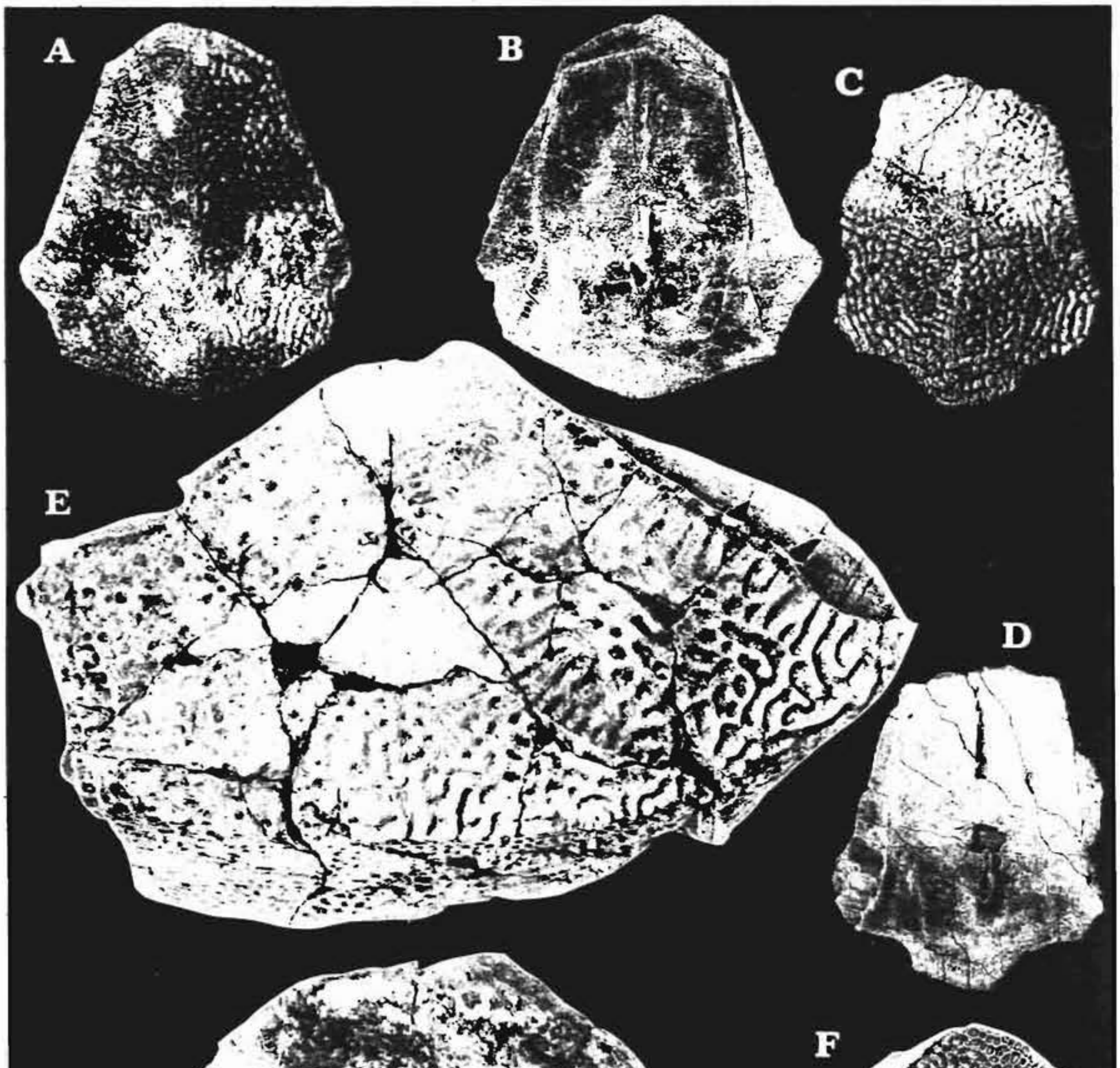
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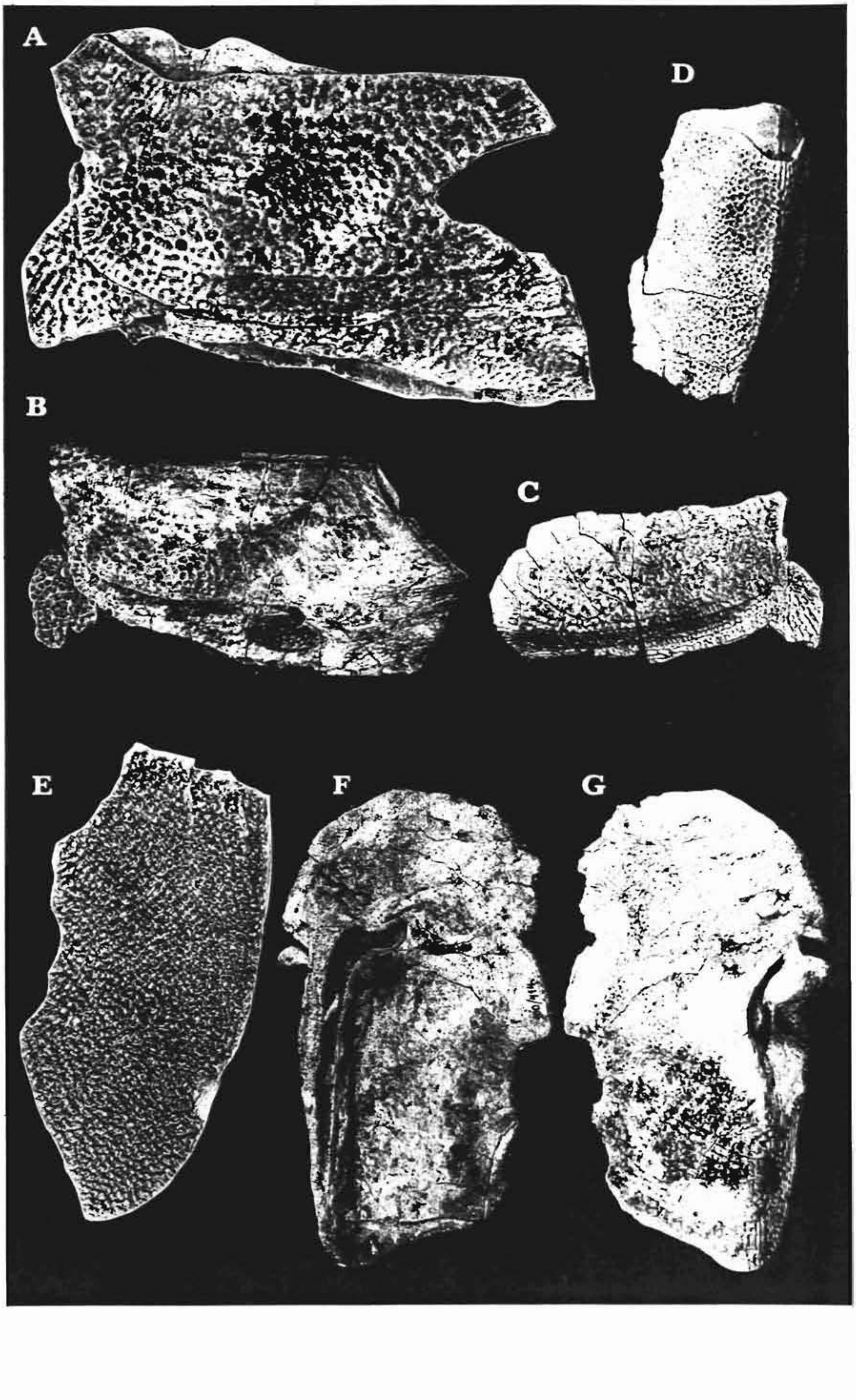
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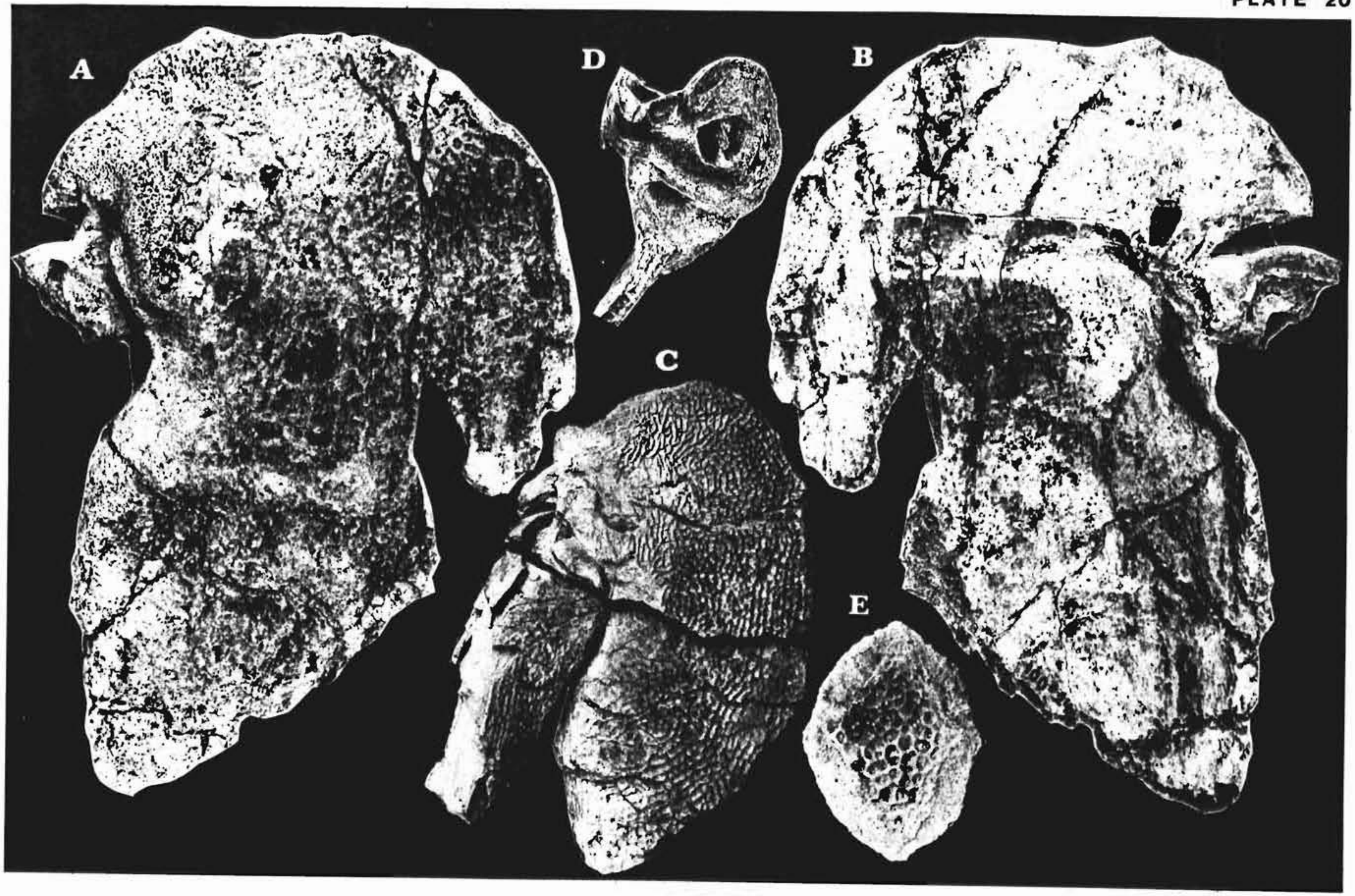
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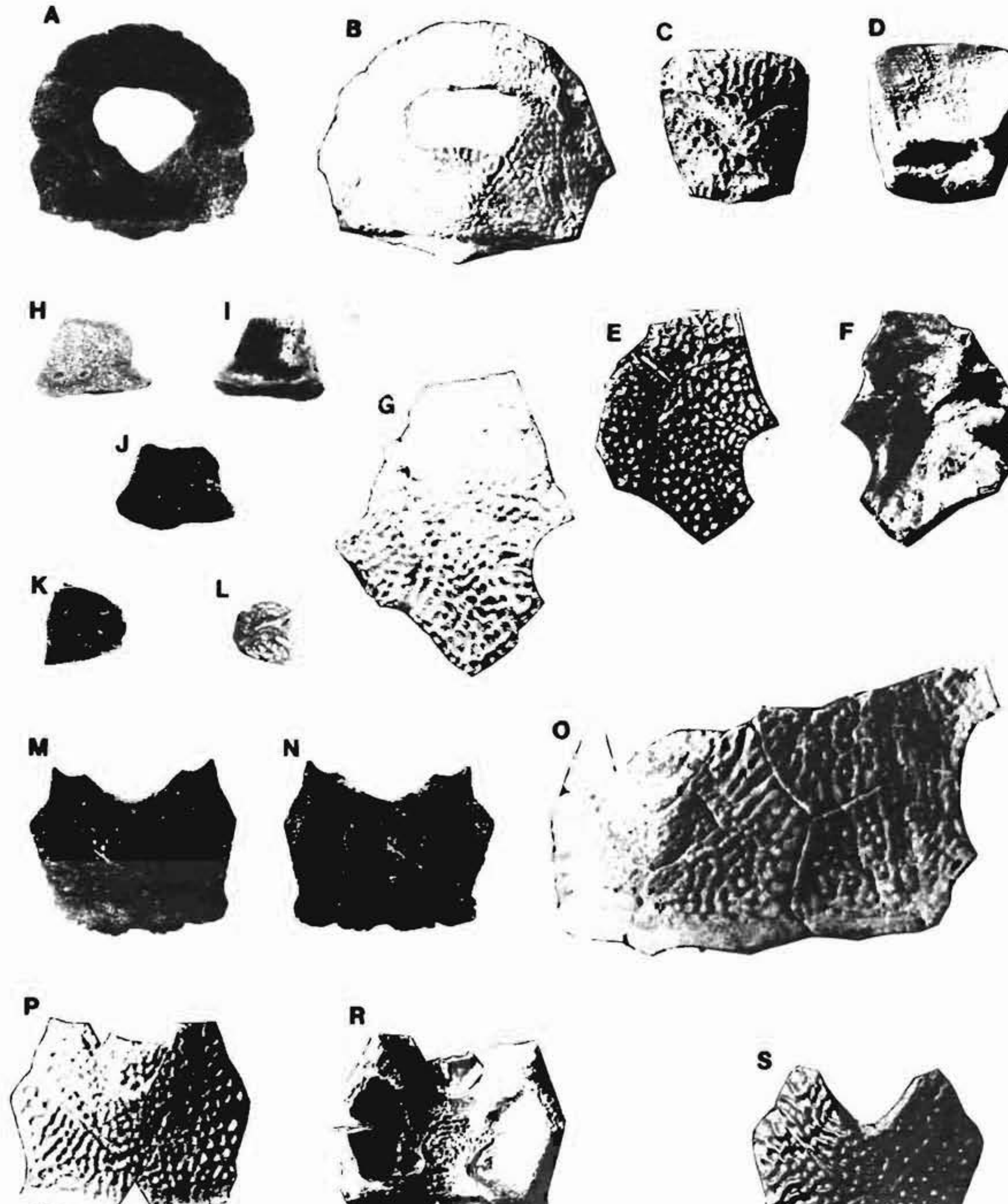
PLATE 22



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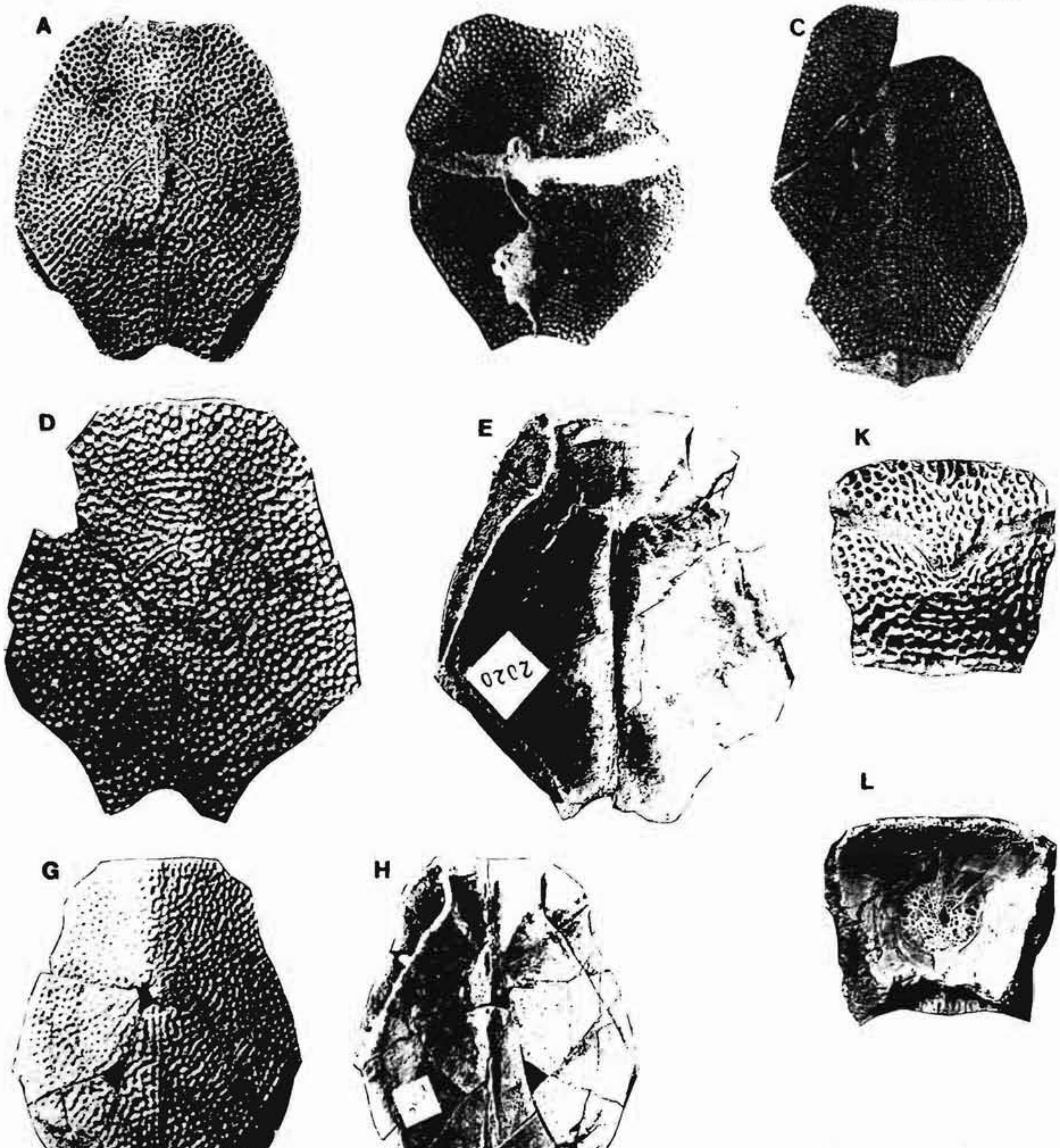

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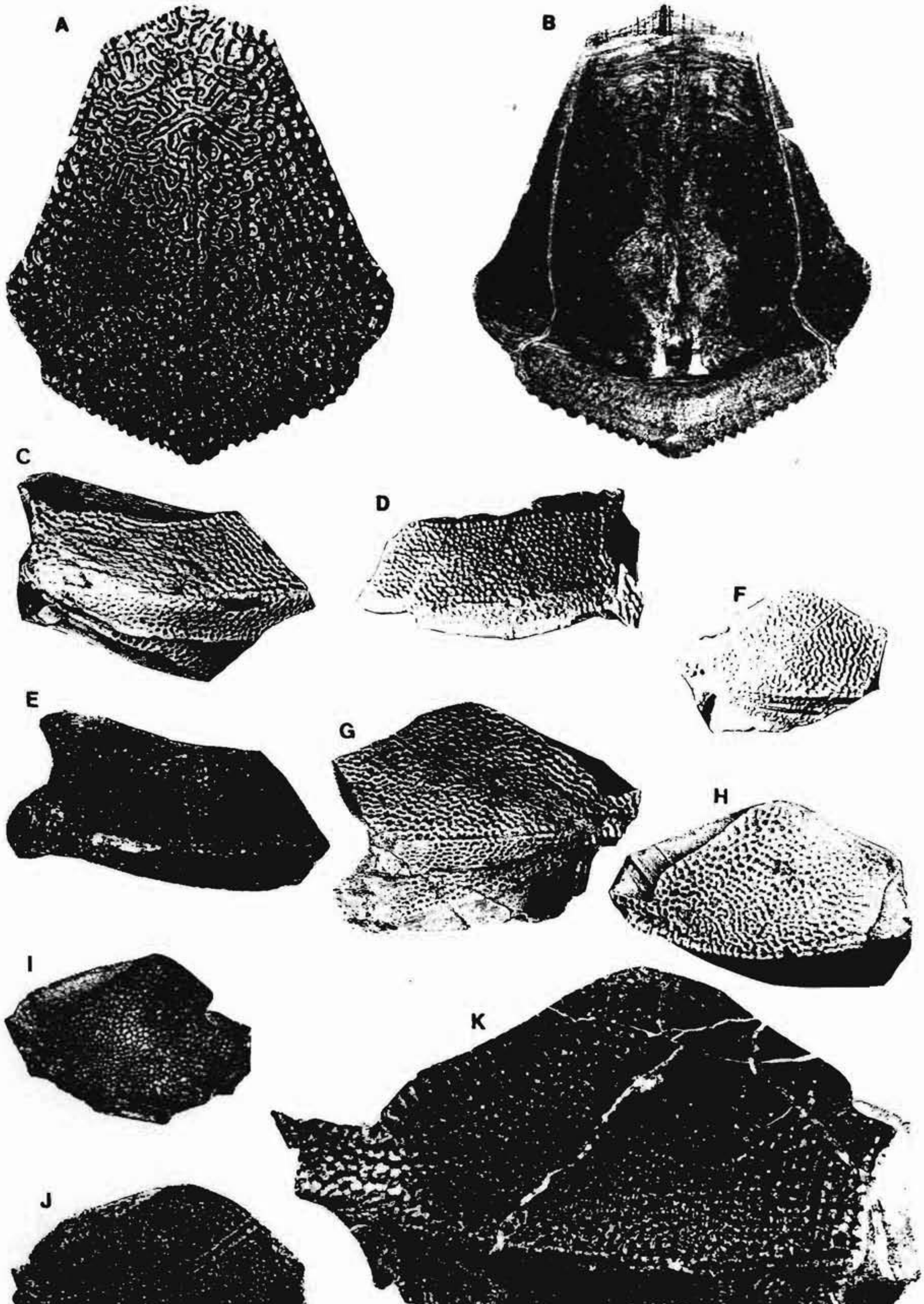

PLATE 25