DISERTATIONES GEOLOGICAE UNIVERSITAS LATVIENSIS
Nr. 21

**IEVA UPENIECE**

# DEVONA BRUŅUZIVJU UN AKANTOŽU PALEOEKOLOĢIJA un to MAZUĻI LODES IEGULĀ

**PROMOCIJAS DARBS**

Doktora grāda iegūšanai ģeoloģijas nozarē

Apakšnozare: pamatiežu ģeoloģija

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DISERTATIONES GEOLOGICAE UNIVERSITAS LATVIENSIS
Nr. 21

**IEVA UPENIECE**

# PALAEOECOLOGY and JUVENILE INDIVIDUALS of the DEVONIAN PLACODERM and ACANTHODIAN FISHES from LODE site, LATVIA

**DOCTORAL THESIS**

In Partial Fulfillment of the Requirements
of the Doctor Degree in Geology
Subdiscipline of Bedrock Geology

UNIVERSITY OF LATVIA

*The doctoral thesis was carried out*:
Chair of Bedrock Geology, Department of Geology, University of Latvia, 1995-2011. This work has been supported by the European Social Fund within the project "Support for Doctoral Studies at University of Latvia" (2010/2011 acad.year).

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This thesis is accepted for the commencement of the degree of Doctor of Geology (in Bedrock Geology) on May, 19 by the Doctoral Commitee of Gelogy, University of Latvia.

The thesis will be defended at the public session of the Doctoral Committee of Geology University of Latvia, on September, 2, 2011, Alberta Street 10, Jāņa un Elfrīdas Rutku auditorium (Room 313).

The thesis is available at the Scientific Library of the University of Latvia Kalpaka Blvd. 4, Rīga, and Academic Library of Latvia, Lielvārdes Street 4, Rīga.

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1. Abbreviations used in text and figures

# Anotācija

Promocijas darbs veltīts unikālu, izcili labi saglabājušos bruņuzivju mazuļu, žokļžaunzivju un dažādu bezmugurkaulnieku izpētei, kurus autore ievākusi ilglaicīgu izrakumu laikā Liepas (Lodes) māla karjerā Latvijā. Materiāla ģeoloģiskais vecums attiecas uz augšdevona Lodes svītu.

Veikta abu izmirušo zivju klašu pārstāvju - bruņuzivju Placodermi un žokļžaunzivju Acanthodii dažādās attīstības pakāpēs esošu mazuļu skeletu izpēte, izveidotas ķermeņu rekonstrukcijas. Izstrādāta to agrīnās ontoģenēzes un attīstības stadiju pētījumu metodoloģija. Katras agrīnās augšanas stadijas izdalīšanai tika noteikts kvalitatīvo un kvantitatīvo īpašību izmaiņu kopums.

Detalizēti aprakstīta devona bruņuzivju mazuļu *Asterolepis ornata* Eichwald sensu Agassiz morfoloģija un bruņu plātņu veidošanās process. Bruņuzivju mazuļiem izdalītas un aprakstītas piecas secīgas agrīnās augšanas attīstības stadijas. Veikta dažādu augšanas stadiju salīdzināšana, lai atšķirīga vecuma vienas sugas bruņuzivis netiktu aprakstītas kā piederošas jauniem, dažādiem zivju taksoniem.

Aprakstīta devona akantožu (žokļžaunzivju) *Lodeacanthus gaujicus* Upeniece morfoloģija un piecas secīgas augšanas stadijas, kas pamatojas uz dažādu izmēru veselu eksemplāru izpēti. Izpētīts zvīņojuma veidošanās process un veikts tā attīstības salīdzinājums ar citiem Acanthodiformes kārtas pārstāvjiem. Izdalītas sešas zvīņojuma zonas, kas ļauj morfoloģiski atšķirīgās zvīņas kļūdaini neaprakstīt kā piederošus jauniem, dažādiem zivju taksoniem.

Izpētīts Lodes laikposma deltu nogulumu ihtiofaunas un bezmugurkaulnieku komplekss. Lodes svītas organismu saraksts papildināts ar jauniem zivju, bezmugurkaulnieku un augu taksoniem. Bruņuzivju mazuļos un akantodēs atrastas un aprakstītas unikālas parazītisko tārpu fosilās atliekas, kas ir senākie līdz šim zināmie zivju parazītu atradumi paleontoloģiskajā hronikā. Tie pārstāv arī senāko mugurkaulnieku-parazītorganismu asociāciju. Tiek sniegts parazītisko tārpu fosilo atlieku salīdzinājums ar mūsdienu parazītiskajiem tārpiem. Tika apstiprināta parazitologa Llewellyn 1982.g. izteiktā hipotēze par parazītisko plakantārpu filoģenēzi senajās zivīs.

Paleoekoloģisko apstākļu izpētei tika veikti organismu atlieku tafonomiskie pētījumi vairākās fosilo zivju iegulās. Lodes karjerā tika izdalīti septiņi tafocenožu tipi saistībā ar nodulumu fācijām.

Pirmo reizi tika rekonstruēta devona deltu zonu paleobiocenozes trofiskā struktūra. Barības ķēžu piramīda pamatojas uz Lodes laikposma visu galveno trofisko līmeņu pārstāvošajiem organismiem: plēsējas un medījamās zivis, bentiskie un planktona organismi, organiskais detrīts un augu atliekas. Organismu barošanās veids tika noteikts morfofunkcionālās analīzes rezultātā, izpētot ķermeņa morfoloģiju, formu, izmērus, kā arī, veicot bruņuzivju mazuļu fosilizētā kuņģa satura pētījumus. Pētījumu rezultātā Lodes paleobiocenozē tika noteikti galvenie zivju barošanās veidi: plēsēji, augēdāji, bentofāgi, plankton- un detrītēdāji.

**Atslēgas vārdi**: ontoģenēze, senie mugurkaulnieki, zivju parazīti, paleoekoloģija, tafonomija.

# Abstract

The promotion work focuses on the investigation of excellently preserved juvenile fish and invertebrate fossils, collected by the author during the long-term excavations in the Liepa (Lode) clay pit, Latvia, where the fossiliferous deposits of the Devonian Lode Formation are exposed. Fossil juvenile fish representing two extinct classes of fishes, Placodermi and Acanthodii, are described and reconstructed. The methodology of studies of early ontogeny and developmental stages of these fishes is developed. A number of qualitatively and quantitatively varying features are defined for the determination of the early growth stages.

The detailed study of morphology of the whole-body preserved juvenile individuals of placoderm *Asterolepis ornata* Eichwald sensu Agassiz is presented. Marked differences in size, shape, proportions and structure of the dermal armour plates and squamation in young fish individuals during the ontogeny are drawn and described, and early stages of growth are distinguished. The comparison of different developmental stages has been made to avoid describing them as the new taxa in the future.

The description of the developmental stages of acanthodian *Lodeacanthus gaujicus* Upeniece is presented and the exact sequence of the early growth is established based on the whole-body preserved specimens of various sizes. Several zones of the scale covering were defined for the various regions of the acanthodian body to avoid the misinterpretation of separate differing scales as belonging to separate taxa.

The faunal list of the Lode Formation is supplemented with the new taxa of fishes, invertebrates and plants. The description of the unique parasitic helminth remains, found within the juvenile fish bodies, as well as the comparison of these remains with recent parasitic helminthes is given. They represent the first finds of remains of parasitic platyhelminthes ever found in the fossil record. The remains belong to the eldest known fish parasites, as well as represent the eldest vertebrate host-parasitic associations known so far.

Taphonomical research on several fish-bearing beds was carried out to investigate the palaeoenvironment of burial. Seven types of taphocoenoses are defined in the Lode pit, which were correlated with the type of lithological types of deposits.

Palaeoecological study of the Lode oryctocoenosis allowed reconstruction the food web and food chains based on morphofunctional analysis of abundant fossils of various taxa. Investigated material comprises the remains of excellently preserved fossils of organisms from different trophic levels: predatory and prey fishes, benthic and planktonic organisms, organic detritus and plant remains, allowing reconstruct a trophic hierarchy. Feeding relations are based on the morphology, body form, size, and investigations of the stomach contents. All feeding modes of fishes are represented, including benthos- and zooplankton feeders, detritivores, herbivores and carnivores. The trophic pyramid typical for the Devonian palaeobiocoenosis of the delta area is created for the first time.

**Key words:** ontogeny, early vertebrates, fish parasites, palaeoecology, taphonomy.

# Introduction

This study is based on the extensive collection of various fossils, collected by the author during long-term excavations (1988-1998, 2001) in the Liepa (Lode) clay pit, Latvia. Outstanding preservation, diversity and abundance of fossils, and the presence of representatives of different trophic levels make the Lode clay pit an outstanding fossil site among the other famous Devonian vertebrate bearing localities in the world (Cloutier, Lelievre, 1998). Particulary unique are finds of juvenile fishes and their parasitic helminthes, which were not known previously in the fossil record.

Excellent preservation of both adult and juvenile fish individuals representing two extinct classes Placodermi (armoured fishes) and Acanthodii (spiny fishes) are of particular importance providing possibilities to determine the developmental patterns and sequence of certain growth stages. Tiny fishes from Lode site represent the first record of juveniles of placoderm fish genus *Asterolepis* (Upeniece, Upenieks, 1992), and are among the smallest and the best preserved antiarch (Vertebrata, Placodermi, Euantiarcha) juvenile individuals ever recorded in the fossil record in the world. A full sequence of growth stages, ranging from the smallest fishes with just ossified dermal armour to advanced juveniles with well ossified bones is presented in the sampled material.

The comparison of *Asterolepis* young individuals with the adult ones was possible based on a long-term investigations of morphology of adult *Asterolepis ornata* (Eichwald, 1840a,b; Pander, 1857; Stensiö, 1931; Gross, 1931, 1933; Karatajute-Talimaa, 1957, 1958b, 1963). A new stage of investigations started when the well-known Latvian geologist, prof. V. Kuršs discovered the whole-bodied adult individuals of *Asterolepis ornata* in Lode pit in 1970 (Kuršs, Lyarskaya, 1973; Lyarskaya, 1977, 1981; Ivanov et al., 1996; Lukševičs, 2001b). *Asterolepis* has also been intensively studied for correlation and assessing the age of rock sequences in East European platform (Gross, 1942; Karatajūte, 1958a, 1963) and in E-Greenland (Marshall, Astin, 1996).

The ontogeny of antiarchs has been studied insufficiently. Stensiö (1948) presented and described some developmental characters of advanced juveniles and subadult individuals of *Bothriolepis canadensis*. Werdelin and Long (1986) described allometric patterns of growth and relationships of various characters for *B. canadensis*. The lack of studies concerning this problem can be explained chiefly by the great scarcity of the material with very low potential to be fossilized.

The ontogenesis of the Devonian acanthodians has not been studied yet. The other known acanthodian juvenile individuals come from the younger, Carboniferous and Permian deposits (Obruchew, 1955; Zidek, 1988; Heidtke, 1990; Zajic, 2005, Beznosov, 2009).

**Topicality and scientific novelty of the study**. Outstanding preservation of both juvenile and adult fish individuals of antiarch placoderms and acanthodians is of particular importance allowing ascertaining the developmental patterns and sequence of the ontogenetic stages. Several ontogenetic stages have been described for the placoderm *Asterolepis ornata* Eichwald sensu Agassiz and acanthodian *Lodeacanthus gaujicus* Upeniece for the first time. Clear distinction and complete description of several growth stages provided during this study are especially significant to avoid misinterpretation of particular specimens belonging to the certain growth stage or different scales of acanthodians as the new taxa in the future.

Lode fossil assemblage contains the remains of organisms representing different trophic levels within the palaeoecosystem of the past, what allowed reconstructing food chains in all trophic levels of the respective palaeobiocenosis. Trophic relations within the food chains characteristic for the deltaic region in the Devonian were traced for the first time. The result of this study demonstrate that the Lode taphocoenosis reflects more diversified food chains in the Devonian in comparison with those which were reported previously (for the Eifelian: Mark-Kurik, 1995; for the Famennian: Lebedev, 1992; Lukševičs, 1992).

The discovery of the Devonian parasitic worm remains within the young fish bodies for the first time in the fossil record (Upeniece, 2001; Poinar, 2003) confirmed the hypothesis (Llewellyn, 1982) on phylogeny of parasitic flatworms in fishes. Such palaeontological evidences as hook systems in placoderm and acanthodian fish young bodies, which have been discovered and tentatively described in the course of this study, prove it.

**The aim of the research is** to study palaeoecology in the submarine part of the Devonian delta and to investigate in detail the early stages of ontogenetic development of placoderm fish *Asterolepis ornata* and acanthodian fish *Lodeacanthus gaujicus*.

The following **main tasks** have been set for achieving the aim:

1) study of the morphology of juvenile individuals of antiarch placoderms *Asterolepis ornata* and of juveniles and adults of acanthodians *Lodeacanthus gaujicus* in details;
2) developing the research methodology of developmental stages in early ontogeny of the antiarch placoderms and acanthodians;
3) implementation of these research methods to elaborate the sequence of ontogenetic stages and developmental patterns of antiarch placoderms and acanthodians;
4) taphonomical research of the Lode fossil assemblage to establish the palaeoenvironment of burial of the organism remains;
5) study of the parasitic helminth remains from placoderm and acanthodian fishes;
6) reconstructing the feeding chains and the trophic pyramid within the palaeobiocoenosis of the Lode time.

### The main theses to be defended

1. Based on the morphological study of the placoderm juvenile fishes from Lode, analyzing changes of the shape, proportions, histological structure and ornamentation of plates of the head-shield, trunk armour and pectoral fins, as well as squamation, it is possible to clarify the "juvenile" features, as well as to confirm the belonging of juvenile fishes to antiarch *Asterolepis ornata* Eichwald sensu Agassiz. Special characters of immaturity are defined for each of the five early growth stages, based on the distinction of the "juvenile" features.
2. Study of the scale morphology, extent of the scale covering, shape and proportions of various bones and parts of the body, and sequence of ossification allow to establish the sequence of ontogenetic growth stages of acanthodian *Lodeacanthus gaujicus* Upeniece. The length of the fin spines may serve as the best indicator of the age of the adult acanthodian *Lodeacanthus*.
3. The studied hooks and hook systems found within the juvenile fish bodies, judging from the morphology and location, as well as comparing with recent animals possessing similar structures, are remains of ancient parasitic helminthes.
4. Morphological and functional analysis of various taxa of animals and plants allow reconstruction of the possible food chains and different trophic levels of the palaeobiocenosis existed in the area of the Devonian delta during the Lode time.

**Approbation of the results.** The main results of the research have been approbated in 30 presentations at 17 international scientific conferences, symposia and congresses, and at 11 domestic scientific conferences at the University of Latvia as follows.

International conferences and congresses:

1. Upeniece I., Upenieks J., 1989. Young Upper Devonian antiarch (*Asterolepis*) individuals from the Lode pit, Latvia. *The 2nd International Colloqium on the Middle Palaeozoic Fishes*. Tallinn.
2. Upeniece I., 1991. Types of fossil fish taphocoenoses of the Lode Formation in Latvia. *The 1st Geological Conference of the Baltic Sea States*. Bulletin of the Geological Survey of Estonia. 1/1: p.13. Tallinn.
3. Upeniece I., 1993. New acanthodians (Acanthodiformes) from the Upper Devonian of Latvia. *The Gross Symposium of fossil fishes*, Göttingen, Germany.
4. Ivanov A., Lukševičs E., Upeniece I., 1993. Squamous part of asterolepid body and placoderm squamation. *The Gross Symposium of fossil fishes*, Göttingen, Germany.
5. Upeniece I., 1995. New species of *Strunius* (Sarcopterygii, Onychodontida) from Latvia, Lode Quarry (Upper Devonian). *8th International Meeting on Early Vertebrates/Lower Vertebrates.* Geobios Memoire Special, M.S. 19: 281-284. Paris.
6. Upeniece I., 1998. The first finds of fossil parasitic flatworms (Platyhelminthes). IGCP 406 meeting *Circum-Arctic Palaeozoic Faunas and Facies*. Ichthyolith Issues Special Publication, 4: 53-55. Warsaw.
7. Upeniece I., 1999. Fossil record of parasitic helminths in fishes. *5th International Symposium on Fish Parasites*. Česke Budejovice.
8. Upeniece I., 1999. The sequence of disintegration of the body of *Asterolepis ornata* (Antiarchi) and associated taphocoenoses. IGCP 406 meeting *Lower-Middle Palaeozoic Events Across the Circum-Arctic*. Ichthyolith Issues Spec. Publ., 5: 48-50. Jūrmala/Rīga.
9. Upeniece I., 2000. The unique fauna of Lode quarry (Devonian, Latvia). IGCP 406 meeting *Pan-Arctic Palaeozoic Tectonics, Evolution of Basins and Faunas.* Syktyvkar, Russia. Ichthyolith Issues Special Publication, 6: 127-133. Syktyvkar.
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11. Upeniece I., Beznosov P., 2002.The squamation of mesacanthid *Lodeacanthus gaujicus* Upeniece. *International Symposium "Geology of the Devonian System"*. Syktyvkar, Russia.
12. Upeniece I., 2002. *Asterolepis* (Placodermi): biogeography, biostratigraphy and habitat. *5th Baltic Stratigraphic Conference "Basin stratigraphy - modern methods and problems"*. Vilnius.
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15. Upeniece I., 2005. Ontogenetic stages of acanthodian *Lodeacanthus gaujicus* Upeniece. IGCP 491 meeting *Devonian vertebrates of the continental margins.* Ichthyolith Issues Special Publication, 8: 24-25. Yerevan, Armenia.
16. Upeniece I., 2005. Types of sutural connections in juveniles and adults of placoderm *Asterolepis ornata*. IGCP 491 meeting *Middle Palaeozoic Vertebrates of Laurussia: Relationships with Siberia, Kazakhstan, Asia and Gondwana* . Ichthyolith Issues Special Publication, 9: 37-41. St.Petersburg.
17. Upeniece I., 2006. Development of exoskeleton of placoderm *Asterolepis ornata* (Frasnian, Latvia). *2nd International Palaeontological Congress. Ancient life and modern approaches*. p. 340-341. Beijing, China.

18. Upeniece I., 2007. Retention of juvenile stages of placoderm *Asterolepis ornata* in adults of other placoderms. *40th Anniversary Symposium on Early Vertebrates/Lower Vertebrates.* Ichthyolith Issues Special Publication, 10: 91-92. Uppsala, Sweden.
19. Upeniece I. 2011. Development of mesacanthid *Lodeacanthus gaujicus* and comparison with other Acanthodiformes. *2nd International Symposium on Early and Lower Vertebrates.* Ichthyolith Issues Special Publication, 12: 50-51. Dallas, USA.

Scientific conferences of the University of Latvia:

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4. Upeniece I., 1995. Jauna devona fosīlo zivju ģints *Lodeacanthus* un tās ontoģenētiskās attīstības stadijas. *LU 54. zin.konf.* Rīga.
5. Upeniece I., 1996. Jauna devona bārkšspuru zivju suga *Strunius kurshi* sp.nov. *LU 55.zin.konf.* Rīga.
6. Upeniece I., 1999. Pirmie parazītisko plakantārpu (Platyhelminthes) atradumi fosīlā veidā. *LU 57.zin.konf.* Rīga.
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8. Upeniece I., 2005. Devona paleoekosistēmas trofiskā struktūra deltu zonā. *LU 63.zin.konf.* Rīga.
9. Upeniece I., 2009. Devona bruņuzivju *Asterolepis ornata* mazuļi un to attīstības stadijas. *LU 67.zin.konf.* Rīga.
10. Upeniece I., 2010. Latvijas vidējā un vēlā devona akantodes. *LU 68. zin.konf.* Rīga.
11. Upeniece I., 2011. Akantožu (Mesacanthidae) ontoģenēze. *LU 69. zin.konf.* Rīga.

The main results of the research have been reflected in 16 scientific publications (five of them – coauthored):

**Papers published in the scientifically cited issues**

1. Upeniece, I. 1995. New species of *Strunius* (Sarcopterygii, Onychodontida) from Latvia, Lode Quarry (Upper Devonian). *In* Lelievre H., Wenz S., Blieck A., Cloutier R. (eds). Premier vertebres et vertebres inferieurs. *Geobios Memoire Special*, M.S. 19, 281-284. Paris.
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6. Ivanov, A., Lukševičs, E., Upeniece, I. 1996. Squamous part of an asterolepid body. *Modern Geology,* vol.20, n. 3-4, 399-409. Amsterdam.

**Other research papers**

7. Upeniece, I. 1998. The first finds of fossil parasitic flatworms (Platyhelminthes). *In* Ginter M., Wilson M. (eds). Circum-Arctic Faunas and Facies. *Ichthyolith Issues Special Publication*, 4, 53-55. Warsaw.
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# 1. Geological background and biostratigraphy of the Lode Formation

## 1.1. Geological setting

The geological structure of the Lode Formation was extensively studied by Prof. Visvaldis Kuršs (1975, 1992a) who singled it out for its distinct lithology and bed geometry, unusual for the Old Red facies. The Lode Formation occurs within a 200 m thick succession of sandstones, siltstones and clays of Middle-Upper Devonian siliciclastics on the Main Devonian Field, and corresponds to the upper part of the Gauja Regional Stage. The deposits of the Lode Formation are preserved for a distance of 160 km along the palaeoslope of the Euroamerican Devonian continent (Kuršs, 1992b, p. 34), extending from the Northern part of Latvia (Cēsis town) to the S-E part of Estonia, and disappear to the West of the Pskov District (somewhere in Pechory Region) in Russia (Fig. 1.1). The Liepa (Lode) clay pit became widely known owing to the exceptionally well preserved fossil fishes discovered by V. Kuršs in 1970.

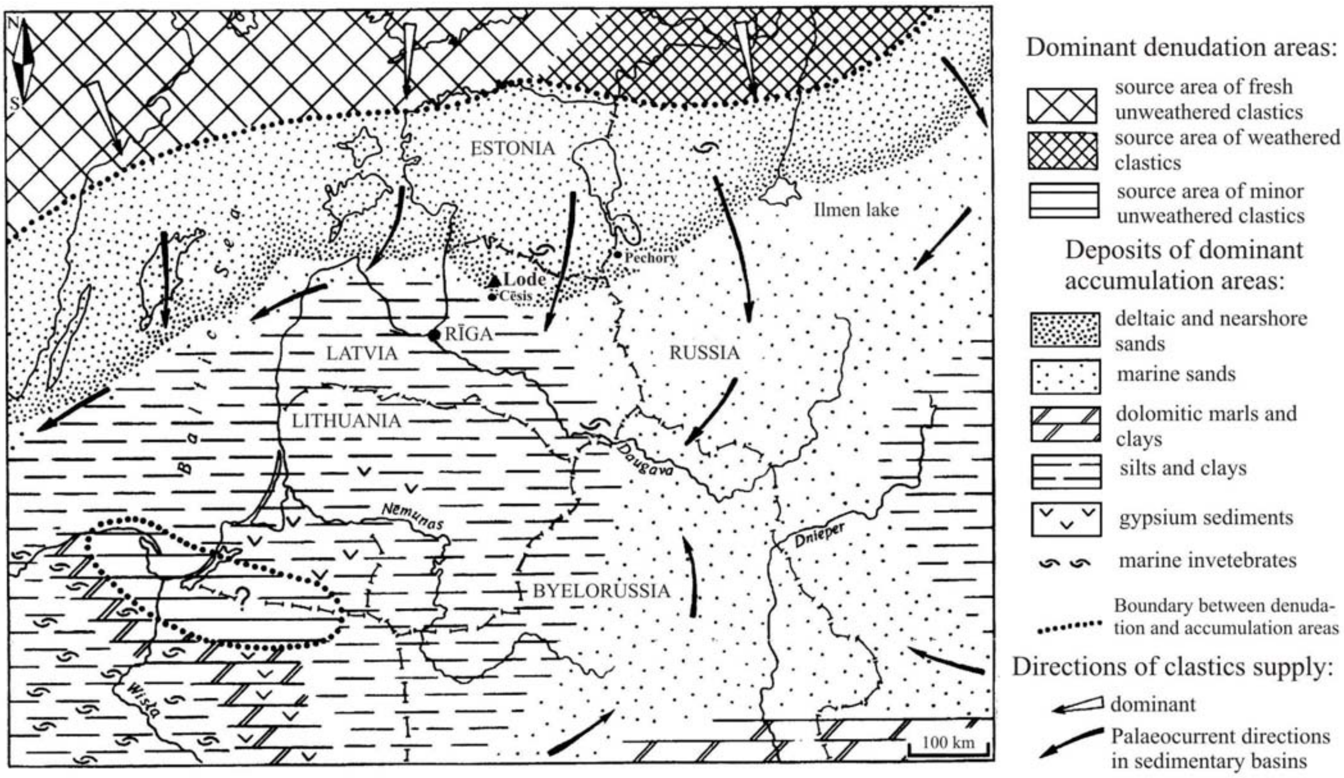


Fig. 1.1. Palaeogeographical map of the Devonian terrigenous sedimentary basin for the late Givetian (Burtnieki Regional Stage) and early Frasnian (Gauja Regional Stage) in the East Baltic (V.Kuršs, 1992 a, Fig. 37 c). The Lode Formation stretches along the paleoslope for a distance between Lode and Pechory (Petseri).

1.1. att. Devona terigēnās sedimentācijas baseina paleoģeogrāfiskā karte Živetas (Burtnieku reģionālais stāvs) un Agrā Franas (Gaujas reģionālais stāvs) stāvam Baltijas austrumu daļā (V.Kuršs, 1992 a, fig. 37 c). Lodes svīta stiepjas gar paleonogāzi virzienā no Lodes līdz aptuveni Pečoriem (Petseri).

The Lode Formation is composed of fine-grained sandstone to clay package which contains large lenses of finely dispersed clays. It covers eroded surface of the middle-coarse grained marine-deltaic sandstones of the Sietiņi Formation (lower part of the Gauja Regional Stage), displayed in Kuršs, 1975, fig. 8; Kuršs, 1992b, Fig. 56. Clayey mud has accumulated in the slump and local bottom depressions on the submarine delta slopes, with brecciated material at the base of depressions. The steep slump scarp reaches 30-70° (Kuršs, 1992 b, p. 33). The meridionally arranged depressions are from several tens to 200-300 metres long. These depressions served as local basins for 'fish sedimentation' (Kuršs, Lyarskaya, 1973). In the central and western parts of Latvia the Gauja Regional Stage is represented only by the Gauja Formation (Kuršs, 1975).

Liepa (Lode) pit is the type locality of the Lode Formation, and exposes a structurally complex sequence, with specific slump and dislocation structures (Fig. 1.2). Individual beds can be traced for several tens to hundreds of metres, but in places their correlation is very problematic due to deformations. The average thickness of the formation reaches 30 m, the maximum 104 m was recorded in a borehole Amata-37 (Kuršs, 1975, p. 34). Lode pit belongs to the brick-producing joint stock company "Lode" and locates near the Liepa village of the Cēsis Region. Sedimentological and taphonomical aspects of the Lode Fm. In the Liepa (Lode) clay pit have been reported in a number of publications (Kuršs, 1975, 1986, 1992a,b; Kuršs, Lyarskaya, 1973; Kuršs et al., 1998, 1999; Upeniece, 1991, 1999d; Zupiņš, 2003).

Sedimentation rates were high in this area, up to 'several metres (?) per year' (Kuršs, 1992a, p.256). Rapid entombment in the fine mud protected the delicate organisms from decay and disintegration, and in turn, the finely grained sediments resulted to a high-extent of fossilization. Stagnant bottom waters presumably might have been developed a toxicity that rendered them uninhabitable by benthic animals, prevented rapid bacterial decay and permitted the accumulation of soft organic matter. Rapid burial could have been influenced by the abnormal silting from land in periods of heavy rains as it was known in modern environments already previously (Gunter, 1947).

To the East from the conventional line connection Bāle sandstone quarry (8 km to the North from the Lode pit) and Pērnava town (West Estonia) the sandstones of the Sietiņi Formation are nearly white and almost without phosphatic remains. Seemingly, that they were completely leached by high chemically active waters due to the high chemical weathering degree of the parent rocks in East Scandinavia which havn't underwent the uplift movements as in West Scandinavia where the crust didn't survive such deep chemical weathering. So outwash clastics in NE Latvia contained silicified plant (*Nematophyton*) debris and a large amount of such chemically stable minerals as quartz, zircon, tourmaline, staurolite and kaolinite (Kuršs, 1992a, 1992b, 1997).

The genesis of the Gauja Regional stage was discussed in Pontén, Plink-Björklund (2007) as well: deposition occurred in a subaqueous to sub-aerial tide-influenced delta plain and front. Deformations are interpreted even of tectonic origin. The author of the promotion work accede with point of view of Prof. V.Kuršs (1992a).

The Middle/Late Devonian boundary problem exists for the whole Baltic region. It has been proposed to assign the Gauja RS to the upper Middle Devonian (Ivanov, 1993; Mark-Kurik *et al.* 1999; Esin *et al.* 2000). The deposits of the Gauja Regional Stage with its *Asterolepis ornata* assemblage in Latvia is assumed to represent terrigenous sedimentation of the earliest Frasnian (Latvian Stratigraphical Commission; Kuršs, 1992b, p.126). The precise

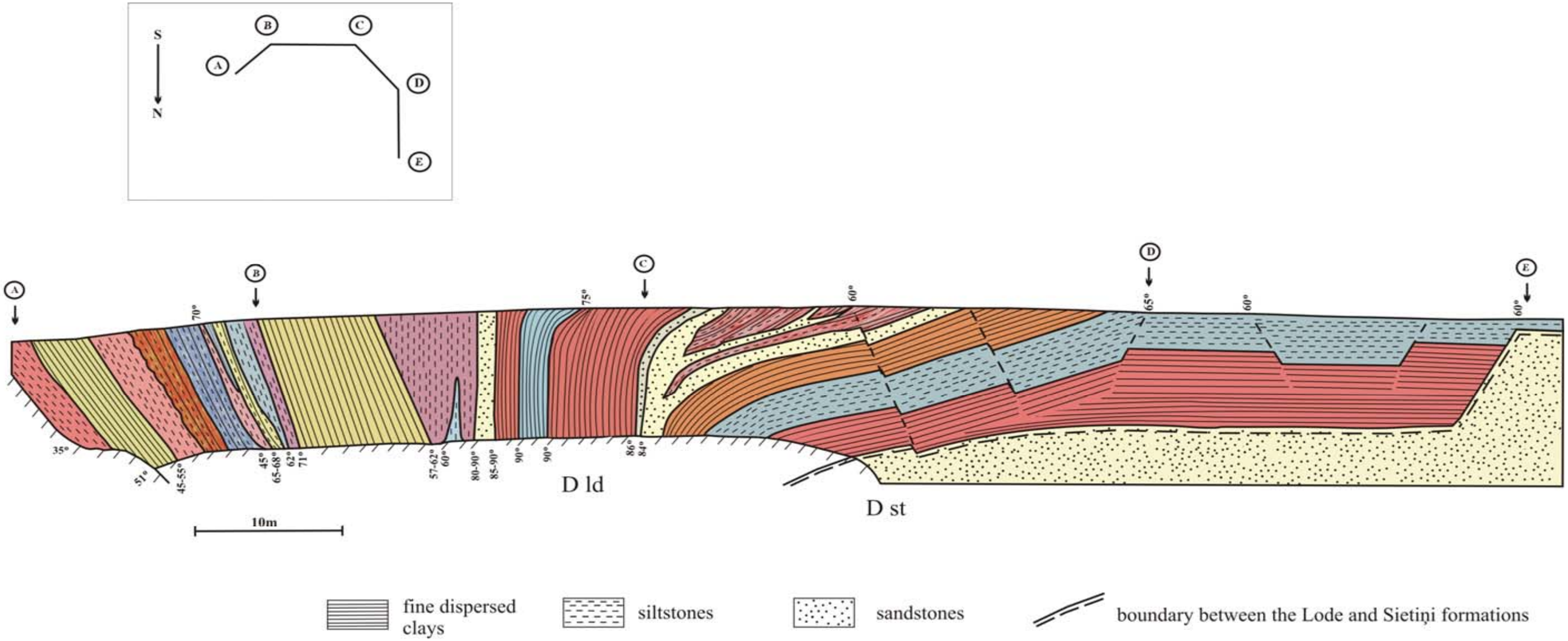


Fig. 1.2. Peculiar section of deposits of the Lode (D ld) and Sietiņi (D st) formations in the Lode pit (1990). Slump processes resulted in deformations and even vertical orientation of beds. Section is semicircular as it follows the clay pit walls; the length of the section is 100 m. Colours approximately correspond to the colouration of rocks.

1.2. att. Lodes un Sietiņu svītas nogulumu savdabīgs griezums Lodes karjerā (1990.g.). Noslīdeņu procesi izraisīja deformācijas un pat vertikālu slāņu sagulumu. Griezuma garums 100 m; griezums ir pusloka formā sakarā ar karjera sienu izvietojumu. Krāsas aptuveni atbilst iežu dabīgajai krāsai.

correlation with miospore or conodont standard zonations remains unclear regarding the stratigraphic position of the Givetian/Frasnian boundary within the Gauja Regional Stage (Mark-Kurik *et al.*, 1999; Blieck *et al.*, 2000; Esin *et al.*, 2000).

Recent detailed sedimentological studies (Pontén, Plink-Björklund, 2007) allowed to propose correlation of the base of the Taghania event dated by the Middle *varcus* conodont zone, with the base of the Lode Fm. (Marschall *et al.*, 2008), hence placing the Givetian/Frasnian boundary even above the Gauja RS. According to Meyen (1987, p.312), the *Archaeopteris* zone in association with *Platyphyllum* characterises the Frasnian-Lower Fammenian. Both plant remains are common fossils in the Lode pit.

### 1.2. Faunal characteristic

Lode fossil site stands out from the most of the Devonian sites in terms of faunal, environmental and paleobiological representativeness, biodiversity and excellent preservation. Lode site has been assessed as one of the most representative fossiliferous sites of the Devonian (Cloutier, Lelievre, 1998).

The Lode pit is famous and unique for the abundance and variety of exceptionally well-preserved Devonian vertebrate and invertebrate fossils, including numerous articulated specimens of juvenile and adult individuals of placoderms, sarcopterygians and acanthodians, remains of parasitic flatforms in bodies of juvenile fishes, abundant eumalacostracans, as well as remains of aquatic and terrestrial plants (Upeniece, 2001b).

Excellent preservation of fossils at the Lode clay pit is the result of anaerobic substrate conditions plus rapid burial in the slump depressions on the submarine delta slopes (Kuršs, 1992 a,b). The completeness of skeletons and minimal distortion of both juvenile and adult fish fossils indicate negligible post-mortem transport. The fast deposition in a clayey mud might have been occurred during slumping events. Intact remains of fishes usually occur in a fine-dispersed clay lenses of various width; disarticulated ones - in fish-bone bearing siltstone/sandstone layers of secondary concentration.

The first fossil fish material in the Lode pit was collected by Dr. L.Lyarskaya in the 1971-72 and 1976 field seasons. Several hundred complete articulated individuals of three fish species were reported by Lyarskaya and Mark-Kurik (1972): the placoderm *Asterolepis ornata* Eichwald sensu Agassiz and sarcopterygians *Laccognathus panderi* Gross, as well as *Panderichthys rhombolepis* (Gross). In addition, isolated plates of *Psammolepis paradoxa* Agassiz were recognized in the red siltstones. Significant dominance of placoderms has been noticed (Lyarskaya, 1972 b, 1981). For the first time fishes belonging to these three species were found as complete skeletons. Previous reconstruction of *Asterolepis ornata* (Gross, 1931) had been based only on the fragmentary material.

Well-preserved plant remains of *Archaeopteris* sp. and *Rhacophyton* sp. have been found as continuous layer on the bedding planes in the basal silty part of the rhythmic deposits (Kuršs, 1992b) and identified by Dr. A.M. Jurina, Moscow University (Lyarskaya, 1981). Two specimens of ostracods *Leperditia* sp. with smooth surface of carapace reaching about 3 mm in length were found in the sandstones of the Sietiņi Formation by L. Lyarskaya (identified by Dr. L. Gailīte in Upeniece, 2001b).

Subsequent excavations in the Lode clay pit added much to the first reported four vertebrata taxa (Upeniece, 1995, 1996, 1998, 1999a,b,c; 2001,b; Upeniece, Upenieks, 1992; Upenieks, 1990; Forey *et al.*, 2000; Zupiņš, 2008). The peculiar "juvenile fish" clay lens was found by the author and Mr. Jānis Upenieks in 1984. Between 1988 and 1998 during annual excavations of the "juvenile fish" fine dispersed clay lens (Fig. 1.3), interbedded within the medium-grained sandstones, the author collected abundant fossils of early vertebrates, invertebrates and plants (Upeniece, 2001b). Organism remains are restricted to grey-coloured organic rich clay laminites. Relative abundance of certain groups such as fishes, mysidaceans, conchostracans and plants appeared. The less common taxa are merostomes and scarcely ostracods, as well as problematic remains.

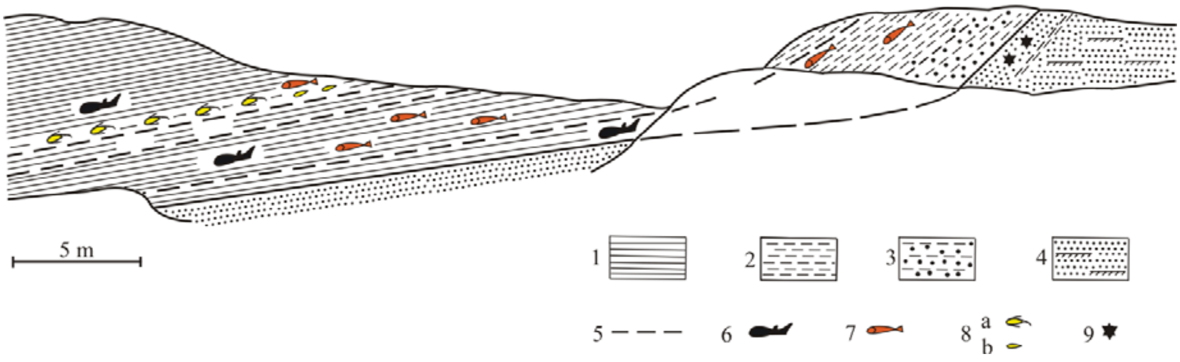


Fig. 1.3. "Juvenile fish" clay lense interbedded within the sandstones in the Lode clay pit (after Kuršs, in: Upeniece, Upenieks, 1992, Fig. 1). 1, clay (mostly greenish-grey), with rare fish fragments and plant macrofossils; 2, silty clay (mostly multicoloured); 3, multicoloured gravelstone-clayey pebbles with clayey-silt cement; 4, massive and cross bedded fine-grained sandstone; 5, layers with numerous finds of Mysidaceans; 6, complete specimens of *Asterolepis ornata*; 7, separate fish bones; 8, juveniles and small fishes: a, complete individuals; b, separate armour plates; 9, sulfide nodules.

1.3. att. "Zivju mazuļu" iegula smilšakmeņos (V.Kurša attēls, publicēts: Upeniece, Upenieks, 1992, Fig. 1). **1**, māli (pārsvarā zaļpelēki), ar retiem zivju atlieku un augu fragmentiem; **2**, aleirītiski māli (pārsvarā daudzkrāsaini); **3**, daudzkrāsaini māla oļi ar mālaini aleirītisku cementu; **4**, masīvi un slīpslāņaini smalkgraudaini smilšakmeņi; **5**, slānīši ar vēžveidīgo Mysidaceans atliekām; **6**, veseli bruņuzivju *Asterolepis ornata* skeleti; **7**, atsevišķi zivju kauli; **8**, zivju mazuļu un sīku zivju atliekas: a, veseli skeleti; b, atsevišķas bruņu plātnes; **9**, sulfīdu konkrēcijas.

An extensive collection of previously unknown juveniles of antiarch *Asterolepis ornata* from Lode is partly described and figured (Upeniece, Upenieks, 1992, Upeniece, 2001b), as well as new taxa of acanthodians and sarcopterygians (Upeniece, 1995, 1996) which will be dealt below. For the first time the parasitic platyhelminth remains were found in the fossil record (Upeniece, 1998,1999 a,b,c, 2001b), which are recognized as the oldest known parasitic remains at all (Poinar, 2003, Table 1). These remains were found in 43 small fish bodies of young individuals of *Asterolepis ornata* and *Lodeacanthus gaujicus* during the study of their morphology. Thousands of crustaceans Mysidaceae (Eumalacostraca) where found in accumulations of several layers (Upenieks, 1990). Presumably they served as a fish food.

The faunal and floral list of the Lode Formation now includes almost all major taxa of vertebrates lived during the Devonian: agnathans, placoderms, acanthodians, actinopterygians and sarcopterygians, with at least 15 species and 13 genera (Table 1.1.). In addition there are at least five major invertebrate groups, and eight taxa of plant macro- and microremains. Coprolites and problematic soft-body organism remains are also common. Ichnofossils occur very rarely.

Six new fish taxa (5 species and 1 genus) have been discovered during the last years (Upeniece, 2001b). Previously unknown genus and species of acanthodian *Lodeacanthus gaujicus* Upeniece, 1996 is represented by juveniles and adults. New species of the sarcopterygians *Strunius* sp.nov. and *Latvius* sp.nov. are recorded (Upeniece 1995, 1996). The first coelacanth from the Baltic Devonian *Miguashaia grossi* has been described by Forey *et al.* (2000), and Zupiņš (2000, 2003, 2008) reported on a complete articulated specimen of sarcopterygian *Eusthenopteron kurshi* Zupiņš and sarcopterygian taphonomy, as well as on important new material of *Glyptolepis baltica* Gross.

Table 1.1. List of animal and plant taxa recovered from the Lode pit, Lode Fm. (Upeniece, 2001 b)
1.1. tabula. Lodes svītas dzīvnieku un augu taksonu saraksts (Lodes karjers) (Upeniece, 2001 b).

| **Vertebrates** | **Invertebrates** | **Plants (aquatic and terrestrial)** |
|---|---|---|
| *Psammolepis alata* Mark-Kurik | Mysidaceae gen.ind. | *Platyphyllum* sp. |
| *Psammolepis paradoxa* Agassiz | Eurypterida indet. | Charales (?) |
| ? *Psammolepis undulata* (Agassiz) | Conchostraca *Pseudestheria* sp. | *Trochiliscus* sp. |
| *Asterolepis ornata* Eichwald sensu Agassiz | Ostracoda indet. | *Svalbardia polymorpha* Høeg |
| *Lodeacanthus gaujicus* Upeniece | Platyhelminthes nov. | *Archaeopteris fissilis* Schmal. |
| *Cheirolepis sp.* | Soft bodied organisms | *Archaeopteris sp.* |
| *Grossipterus crassus* (Gross) | | *Rhacophyton sp.* |
| *Miguashaia grossi* Forey et al. | | |
| Coelacanthidae gen.et sp.indet. | | |
| *Strunius* sp.nov. | | |
| *Glyptolepis baltica* Gross | | |
| *Laccognathus panderi* Gross | | |
| *Latvius* sp.nov. | | |
| Osteolepididae gen.et sp.indet. | | |
| *Eusthenopteron kurshi* Zupiņš | | |
| *Panderichthys rhombolepis* (Gross) | | |

The placoderm *Asterolepis ornata* is the most abundant component of vertebrate fauna: both adult and juvenile individuals (Upeniece, 2001b). An extensive collection of juveniles of the antiarch *Asterolepis ornata* from Lode was partly described and figured by Upeniece and Upenieks (1992). Some 35 adult *Asterolepis ornata* bodies, disintegrated to different degrees, were exposed in 1988, allowing study of the disarticulation process (Upeniece, 1999b). Several plates of *Psammolepis alata* Mark-Kurik were also exposed. The lack of small juveniles of *Asterolepis ornata* in other fish-bearing clay lenses probably reflects the existence of separate areas of hatching of the youngs. Juveniles may have lived in shallows and might have not associate with large fish.

The majority of *Asterolepis ornata* remains from exposed beds in Lode pit must have reflect the paleoenvironments. The genus *Asterolepis* is known from continental (Scotland, Greenland, Spitsbergen, New-York) and marine sediments (Baltic, Belgium, France, Iran, Nevada) (Gross, 1931, 1933a, 1940, 1965; Watson, 1932; Stensiö, Save-Söderbergh, 1938; Nilsson, 1941; Karatajūte-Talimaa, 1963; Wells, 1964; Miles, 1968; Murphy et al., 1976; Gregory et al., 1977; House et al., 1977; Denison, 1978; Janvier, 1979; Lyarskaya, 1981; Lelievre et al., 1988; Blieck, Lelievre , 1995; Ivanov, Lukševičs, 1996; Marshall, Astin, 1996; Schultze, Cloutier, 1996; Mark-Kurik, 2000). Either *Asterolepis* inhabited both types of environments (lakes, rivers and marine deltaic regions) or remains of continental origin were accumulated also in nearshore margins of epicontinental basins is not clear. Possibly asterolepids, as well as acanthodians were catadromous fishes who migrate into the sea at breeding time. Allochthonous organisms from terrestrial and fresh-water environments (e.g. plants, conchostracans) were transported into the depressions, and there is a possibility of fresh-water influence.

The complete list of papers dedicated to fossil fish from the Lode pit (1972-2008) includes Lyarskaya, 1972b, 1977, 1981; Lyarskaya, Mark-Kurik, 1972; Kuršs, Lyarskaya, 1973; Worobjewa, 1973, 1975; Vorobyeva, 1980, 1989, 1995; Vorobyeva, Schultze 1991; Kuršs, 1975, 1986, 1992b; Upeniece, 1991, 1993, 1995, 1996, 1998, 1999 a,b,c,d, 2000, 2001 a,b, 2002 a,b, 2003, 2005 a,b,c, 2006; Upeniece, Upenieks, 1992; Upeniece, Beznosov, 2002; Lukševičs, 2001; Ivanov, *et al.*, 1996, Ahlberg, *et al.*, 1996; Forey, *et al.*, 2000; Zupiņš, 2000, 2003, 2008.

### 1.3. Comparison with similar ichthyofaunas from other areas

The whole Devonian sequence in the Main Devonian Field (East Baltic area: Estonia, Latvia, Lithuania, N-W part of Russia and Byelorussia) nowadays contains more than 270 different taxa at the specific stratigraphic level (Esin et al., 2000; Mark-Kurik, 2000). Upper Givetian-Lower Frasnian sequence in the Main Devonian Field corresponds to the Gauja, Amata and Pļaviņas regional stages characterized by overall similar ichthyofaunas, and the ichthyofaunas resemble those from several other areas (Table 1.2).

The specific and generic composition of the organism assemblage from the Gauja Regional Stage resembles that from the Amata and Pļaviņas regional stages of the Main Devonian Field:

1) Gauja and Amata regional stages comprise 10 common and stratigraphically limited species: *Psammolepis venyukovi, Ps. undulata, Plourdosteus livonicus, Devononchus concinnus, D. laevis, Homacanthus gracilis, Nostolepis gaujensis, Glyptolepis baltica, Laccognathus panderi,* and *Panderichthys rhombolepis*. These regional stages represent similar terrigenous facies and yield no conodonts to determine the precise position of the Givetian/Frasnian boundary.

2) Amata and Pļaviņas regional stages comprise four common and stratigraphically limited species: *Psammosteus praecursor, Ps. maeandrinus, Ps. asper*, and *Asterolepis radiata*. Eight shared genera are known: *Psammosteus, Plourdosteus, Asterolepis, Bothriolepis, Glyptolepis, Laccognathus, Holoptychius*, and *Eusthenopteron*. The sets of the facies are different: terrigenous for the Amata RS and mainly carbonate for the Pļaviņas RS.

3) Gauja and Pļaviņas regional stages comprise 10-12 shared genera: *Psammosteus, Plourdosteus, Asterolepis, Bothriolepis* (?), *Haplacanthus, Glyptolepis, Laccognathus, Holoptychius* (?), *Panderichthys, Latvius, Eusthenopteron,* and *Strunius*.

The Gauja RS comprise five transition species from the upper Givetian (Burtnieki Fm.) in common within the Main Devonian Field: *Ganosteus stellatus, Haplacanthus marginalis, Rhadinacanthus multisulcatus, Homacanthus gracilis,* and *Grossipterus crassus* (Table 1.2).

Outside the Main Devonian Field the most similar Late Devonian assemblages are known from the South, Middle and North Timan sections (Ivanov, Lukševičs, 1996); eight species occur within the lower Frasnian deposits: *Psammolepis* cf. *undulata, Psammosteus praecursor, P. maeandrinus, P.* cf. *cuneatus, Plourdosteus* ex gr. *mironovi, Asterolepis radiata, Bothriolepis obrutschevi,* and *B. cellulosa*. At least 11-12 genera are similar to the vertebrates of the Gauja Regional Stage (Table 1.2): *Psammolepis, Psammosteus, Plourdosteus, Asterolepis, Bothriolepis* (?), *Devononchus, Haplacanthus, Homacanthus, Glyptolepis, Laccognathus, Holoptychius,* and *Latvius*.

The equivalent of the Gauja Regional Stage is absent in the Scottish sequence (Ahlberg *et al*., 1999). Two species from the Givetian?/Frasnian of Scotland are similar to those from the Main Devonian Field: *Psammolepis undulata* (similar to those from Gauja and Amata regional stages), *Plourdosteus mironovi* ? (known from Pļaviņas Regional Stage also) and six to seven genera: *Psammolepis, Plourdosteus, Asterolepis, Bothriolepis, Laccognathus, Panderichthys*?, and *Eusthenopteron*. The late Givetian vertebrate genera of Scotland well coincide with those from the Baltic area: *Watsonosteus, Microbrachius, Dickosteus*?, *Millerosteus*?, and *Homostius* (Ahlberg *et al*., 1999).

The assemblages of fishes of the early Frasnian regional stages of the Main Devonian Field (Esin *et al*., 2000; Mark-Kurik, 2000) on the generic levels are similar to the assemblages from the Frasnian Escuminac Formation, Miguasha (Schultze, Cloutier, 1996) as follows:

1. The Gauja RS share four to six genera: *Cheirolepis, Plourdosteus, Miguashaia, Bothriolepis* (?), *Eusthenopteron,* and *Holoptychius* (?).
2. The Amata RS contain five shared genera: *Cheirolepis, Bothriolepis, Plourdosteus, Holoptychius,* and *Eusthenopteron*. The most important fossil site is the locality Pastamuiža at Daugava River, Latvia.
3. The Pļaviņas RS contains four shared genera: *Bothriolepis, Plourdosteus, Holoptychius,* and *Eusthenopteron.* The most important fossil site is the locality Koknese (Kokenhusen).

"Stensiö (1948) correlated the Escuminac Fm. with the *Cellulosa* marl (Pļaviņas RS) of Latvia based on the presence of the antiarch *Bothriolepis canadensis* and *B. cellulosa*, respectively" (Cloutier *et al*., 1996, p.191). The megaplant fossils of *Archaeopteris halliana* and *A. obtusa* are known from the Escuminac Fm. The *Archaeopteris fissilis* is characteristic for the Lode Fm. The genus *Archaeopteris* characterises the Frasnian - early Fammenian, as already mentioned above.

The above mentioned three regional stages comprise similar genera also to the Frasnian Okse Bay Formation, Ellesmere Island, Canada (Cloutier, Lelievre, 1998) as follows: *Psammosteus, Glyptolepis, Holoptychius,* and *Bothriolepis*. Two genera *Strunius* and *Latvius*, are similar to those from the Frasnian of the Oberer Plattenkalk Formation, Bergisch-Gladbach, Germany (Cloutier, Lelievre, 1998). In conclusion, the fish fauna of the Gauja RS is more similar to the Frasnian faunal assemblages of the Main Devonian Field, Timan, Scotland, and of Miguasha, than to faunas of the late Givetian age. Presumably, the Gauja RS is of lower Frasnian age. Nevertheless, this Middle/Upper Devonian boundary problem still exists, as mentioned previously.

Table 1.2. Comparison of the Gauja Regional Stage vertebrates with those from the Upper Givetian and lowermost Frasnian formations of the Main Devonian Field, lowermost/Middle Frasnian of Miguasha and the Upper Givetian/lower Frasnian of Scotland and Timan correspondingly to the placoderm zonation of the Main Devonian Field (Upeniece, 2001, Table 2, with modifications) (after Ahlberg *et al*., 1999; Cloutier *et al*., 1996; Dineley, Loeffler, 1993; Esin *et al*., 2000; Ivanov, Lukševičs, 1996; Schultze, Cloutier, 1996; Valiukevičius, 1998).

1.2. tabula. Gaujas reģionālā stāva mugurkaulnieku taksonu salīdzinājums ar Galvenā Devona lauka (augšējās Živetas/apakšējās Franas), Miguašas (apakšējās/vidējās Franas), Skotijas un Timāna (augšējās Živetas/apakšējās Franas) mugurkaulnieku taksoniem saistībā ar Galvenā Devona lauka zonējumu pēc bruņuzivīm (Upeniece, 2001, Table 2, with modifications) (dati pēc: Ahlberg *et al*., 1999; Cloutier *et al*., 1996; Dineley, Loeffler, 1993; Esin *et al*., 2000; Ivanov, Lukševičs, 1996; Schultze, Cloutier, 1996; Valiukevičius, 1998).

| Stage, Reg. Stage/Form., Placoderm zonation | Main Devonian Field | | | | | | Miguasha | Scotland | | South, Middle, North Timan | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Upper Givetian ? | | Lower Frasnian | | | | L / M Frasnian | Upper Givetian ? | lower Frasnian | upper Givetian / lower Frasnian | lower Frasnian |
| | Aruküla | Burtnieki *A. dellei, Watsonosteus* | Gauja Reg. Stage *A. ornata* zone | | Amata *B. prima-obruchevi* zone | Pļaviņas *B. cellulosa* zone | Escuminac | Nairn Beds, (correlates with Amata) | Whitemire, Boghole (cor. with Plaviņas) | *A. ornata, B. prima-obruchevi* zone | *B. cellulosa* zone |
| Vertebrata taxa from Gauja RS | | | Sietiņi Fm. (Gauja Fm. in C,W-Latvia) | Lode Fm. | | | | | | | |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| *Ganosteus* | - | *G. stellatus* | *G. stellatus* | - | - | - | - | - | - | - | - |
| *Psammolepis* | *Ps. proia* | *Ps.abavica*<br>*Ps.* sp. | *Ps. venyukovi,*<br>*Ps. undulata,*<br>*Ps. paradoxa,*<br>*Ps. alata,*<br>*Ps. heteraster* | *Ps. paradoxa,*<br>*Ps. alata,* | *Ps. venyukovi,*<br>*Ps. undulata* | - | - | *Ps.undulata* | - | *Ps.* cf. *undulata*<br>*Ps.* sp. | *Ps.* sp. |
| *Psammosteus* | - | *P. bergi,*<br>*P.* sp. | *P.* sp. | - | *P. praecursor,*<br>*P. maeandrinus?*<br>*P. asper,*<br>*P. levis,*<br>*P. cuneatus,*<br>*P. livonicus* | *P. praecursor,*<br>*P.maeandrinus*<br>*P. asper* | - | - | - | *P. praecursor*<br>*P. maeandrinus,*<br>*P.* cf. *cuneatus* | *P. praecursor,*<br>*P. maeandrinus,*<br>*P.* sp. |
| *Plourdosteus* | - | *Pl.* sp. | *Pl. livonicus* | - | *Pl. livonicus* | *Pl. mironovi* | *Pl.canadensis* | *Pl.? magnus* | *Pl. mironovi?* | - | *Pl.* sp., *Pl.*. sp.nov.<br>*Pl.* ex gr. *mironovi* |
| *Asterolepis* | *A. estonica* | *A. dellei,*<br>*A. essica,*<br>*A.*sp. 1 | *A. ornata* | *A. ornata* | *A. radiata* | *A. radiata* | - | *A. maxima* | *A.* sp. | *A. radiata* | *A. radiata* |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bothriolepis ?* | - | - | *B.* sp. ? | - | *B. prima,*<br>*B. obruchevi* | *B. cellulosa*<br>*B. panderi* | *B. canadensis* | - | *B.gigantea,*<br>*B.* sp. | *B. obruchevi,*<br>*B.* sp. | *B. obruchevi,*<br>*B. cellulosa,*<br>*B.* sp.,<br>*B.* sp.n. A |
| *Devononchus* | - | - | *D. concinnus,*<br>*D. laevis* | - | *D. concinnus,*<br>*D. laevis* | - | - | - | - | *D.* sp. | *D.* sp. |
| *Haplacanthus* | *H. marginalis* | *H.marginalis* | *H. marginalis, H. ehrmanensis* | - | - | *H. perseensis* | - | - | - | - | *H.* sp. |
| *Nodocosta* | *N. pauli* | - | *N. pauli* | - | - | - | - | - | - | - | - |
| *Rhadinacanthus* | *R. multisulcatus* | *R.. multisulcatus* | *R. multisulcatus* | - | - | - | - | - | - | - | - |
| *Homacanthus* | *H. gracilis* | *H.talavicus* | *H. gracilis* | - | *H. gracilis* | - | - | - | - | - | *H.* sp. |
| *Nostolepis* | - | - | *N. gaujensis* | - | *N. gaujensis* | - | - | - | - | - | - |
| *Lodeacanthus* | - | - | - | *L. gaujicus* | - | - | - | - | - | - | - |
| *Glyptolepis* | *G.*sp. | *G.*cf. *paucidens,*<br>*G.*sp. | *G. baltica,*<br>*G.* sp. | *G. baltica* | *G. baltica* | *G.*sp. | - | - | - | *G.* sp. | *G.*sp. |
| *Laccognathus* | - | *L.* sp. | *L. panderi* | *L. panderi* | *L. panderi* | *L.* sp. | - | *L.* sp. | *L.* sp. | *L.* sp. | *L.* sp. |
| *Holoptychius* | - | - | *H.* ? sp. | - | *H.*cf. *nobilissimus* | *H.*cf.*nobilissimus* | *H. jarviki* | - | - | *H.* sp. | *H.*cf.*nobilissimus,*<br>*H.* sp. |
| *Panderichthys* | - | *P. ?* sp. | *P. rhombolepis* | *P. rhombolepis* | *P. rhombolepis* | - | - | *P.? leptognathus* | - | - | - |
| *Latvius* | - | - | - | *L.* sp.n. | - | *L. grewingki* | - | - | - | - | *L.* sp. |
| *Eusthenopteron* | - | - | - | *E. kurshi* | *E. obruchevi* | *E. saevesoederberghi* | *E foordi* | - | *E. traquairi* | Eusthenopteridae gen.ind. | - |
| *Strunius* | - | - | - | *S.* sp.nov. | Struniiformes gen.indet. | *S. rolandi* | - | - | - | Struniif. gen.indet. | Struniif. gen.indet. |
| *Grossipterus* | - | *G. crassus* | *G. crassus* | - | - | - | - | - | - | - | - |
| *Miguashaia* | - | - | *M.* sp. * | *M. grossi* | - | - | *M. bureaui* | - | - | - | - |
| *Cheirolepis* | *C.* sp. | *C.gaugeri* | - | *C.* sp. | *C.* sp. | - | *C.canadensis* | - | - | - | - |
| Osteolepididae g.ind. | | | | | | | | | | | |
| Dipteridae g.ind. | | | | | | | | | | | |

* - *Miguashaia* sp. is known from Ērmaņi outcrop, river Gauja, near Līgatne (Cloutier *et al.*, 1996, after Ørvig 1957).

# 2. Material and methods

This study is based upon collection of fossils during the long-term excavations of the field seasons of 1988-1998 and 2001, elaborated by the author in the Lode clay pit at Liepa in the Northern Latvia, where the Upper Devonian, Lower Frasnian Lode Formation is accessible for studies. During the fieldwork the detailed geological sections was compiled, taphonomical data were obtained and an extensive collection of fossil remains belonging to various taxa of animals and plants has been gathered.

The Lode Formation was examined by the author at four another localities also. Less spectacular exposures are found along the river Raunis (excavations in 1998 and 2003), in the Ķūķi outcrop at the river Gauja (excavations in 2001), in Glūda old deposit locality (now within the Cēsis city; excavations in 1989 and 2001), Pechori pit (Russia; excavations in 1989). A good preservation of fossils is to be expected in Gāršas clay deposit, where placoderm *Asterolepis ornata* remains are known from the boreholes (Kuršs, 1975).

## 2.1. Examined fish and invertebrate material

The material examined includes an extensive collection of number of specimens of various taxa. The majority of fossil material comes from the so-called `juvenile fish` clay lens interbedded within the sandstones. The Lode fossil assemblage consists of the well-preserved vertebrate, invertebrate and plant remains representing organisms from different habitats.

The ***vertebrate collection*** includes various and almost all major Devonian fish taxa: placoderms, acanthodians, sarcopterygians, and actinopterygians. Most finds represent fish of small size and young individuals of the both extinct fish classes: placoderms and acanthodians.

The collection of more than 300 specimens of articulated and disarticulated young individuals of excellently preserved **placoderm** antiarch *Asterolepis ornata* Eichwald sensu Agassiz, 1840 represents the individuals at varying stages of growth, ranging from recently ossified dermal armour to advanced juveniles. The collection is stored in the Natural History Museum of Latvia (LDM), Riga, collection No. LDM 260. All specimens are of small size and supposedly belong to juveniles with the length of the dermal armour comprising about 1 to 4 cm. Disarticulated individuals, scattered skeletal parts and separate plates are more useful for investigations, due to the obscured overlapping areas of the plates in articulated individuals. Over than 200 separate armour plates were also collected; most of them are well preserved and complete enough to be measured with sufficient accuracy. Almost all the dermal bones presented in the antiarch skeleton have been found among the material. The first juveniles were discovered in 1986.

Subadult individuals are rare finds. Some detached armour plates of subadult individuals of *A. ornata* have been reported before, for example, Gross mentioned two AMD plates comprising 24 and 35 mm in the length (Gross, 1940, p.24). The length of the dermal armour of these subadult individuals could be estimated at about 50 mm and little over 70 mm, respectively. Poor data on the subadult individuals do not allow the detailed reconstruction of the entire sequence of the ontogeny of the exoskeleton of *A. ornata*. However, the advanced juvenile individuals don't have marked morphological distinctions from the adults and subadults, therefore the lack of the medium-sized specimens aren't a great shortage.

Adult individuals of *Asterolepis ornata* are well represented by many articulated specimens from the Lode pit, collected by L. Lyarskaya, but disarticulated complete armour plates, necessary for comparison with juveniles, were rarely collected there. Extensive material of articulated adult individuals stored in the Natural History Museum of Latvia (collections No LDM 43 and LDM 55) was examined and measured for comparison purposes. Some figured specimens come from the private collection of Mr. J. Upenieks. They are prefixed with UP.

Comparative study of the Devonian fossil fish collections from the museums in Sweden and China was elaborated. The following studies on the related antiarch placoderm material have been done in the Swedish Museum of Natural History in Stockholm: on the stages of disintegration sequence of carcasses of the *Bothriolepis canadensis* (in 1998), on the ornamentation of the plates in the early subadult stage of *Pterichthyodes milleri,* as well as on the preserved stomach content on the same small individual of *Pterichthyodes* (in 2007). The other comparative studies have been done on the yunnanolepiform-like antiarchs *Minicrania lirouyii, Heteroyunnanolepis qujingensis, Chuchinolepis gracilis*, housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (in 2006).

The collection No LDM 270 consisting of more than 60 individuals of excellently preserved **acanthodians** *Lodeacanthus gaujicus* Upeniece, 1996 from the Lode pit represents articulated and disarticulated juvenile and adult individuals of small size, reaching up to 4 cm in length. The smallest individual comprises 0.8 cm in the length and it represents the smallest known acanthodian in the fossil record ever found. The longest individual presumably represents the adult form.

The ***invertebrate collection*** includes countless representatives of various taxa of the well-preserved crustaceans: mysidaceans and conchostracans, as well as small amount of ostracods. Eurypterids occur only as fragmental material. Particularly significant are 77 specimens of parasitic helminth remains within the 43 juvenile fish bodies of the above mentioned placoderms and acanthodians, representing the eldest fish parasites and the eldest host-parasitic associations ever found in the fossil record.

## 2.2. Field study methods

The detailed, 12 m high geologic section of the Lode Formation including the `juvenile fish` clay bed was constructed and supplemented for all taxa which have been found during several years. Additionally hand-drilling method was used to reach the deposits below the ‘juvenile fish’ bed in 1998. The variegated fine-dispersed clays were traced down to 2.7 m deep. The same deposits with the same type of the crustacean taphocoenosis occurred also on the slope of the depression, where the clay filled lens forms steep layers (30-$45^0$) on the margin of the slope. The lowermost, non-fossiliferous part of this lens (to depth of 4.62 m) was described based on the exposed section of steeply laying layers of variegated silty and sandy clay, siltstone, as well as intercalated sandstone near the sandstone margin of the clay-filled depression.

### 2.3. Methods of morphological research

**Preparation** of fish fossils has been limited only to mechanical work with very sharp steel needle under the binocular microscope due to softness of clay and fragility of the bone. The preparation of the delicate structures of the caudal part of placoderm juveniles was practically impossible due to fragility of the material. Photographs were made using digital camera Nicon Coolpix 4500.

**Measurements** of the dermal armour plates of the head shield, trunk armour and pectoral fins of placoderm juvenile individuals were made in accordance with the system offered by Karatajūte-Talimaa (1963), modified by Werdelin, Long (1986) with some additions for juvenile characters of individuals. Ratios were calculated for studies of allometry.

Measurements of placoderm juveniles were taken to the nearest 0.05 mm using the ruler of binocular, of adults - with Vernier caliper to the nearest 0.5 mm. The measurements of the width for the armour plates having two equal laminae (AMD, PMD of placoderms) were taken in a straight line for each lamina. Nevertheless, it is possible that post-mortem changes could have slightly influenced the accuracy of measurements.

The measurements of body parts and fin spines of acanthodians were made in accordance with the system, proposed by Zidek (1976). The length of the fin spines turned the best for the determination of the agedness than the total body length of acanthodian *Lodeacanthus gaujicus*: the scale covering of the body must have been easily undergone deformation although only some specimens are expanded or twisted. Therefore all dimensions regarding the length of the body are estimated.

**Terminology** used herein for placoderms follows Stensiö (1948) with some slight alterations suggested by Miles (1968), and some additions by Young (1983, 1988), Young, Gorter (1981) and Janvier (1996). It also adopts homologies proposed by Young (1984 b) for cheek and jaw plates. Several new terms are introduced for structures not previously described in antiarchs: additional ridges on the head-shield, lateral and ventral wall armour plates (latter in: Upeniece, Upenieks, 1992, fig. 3.A); they are explained in the text and figures. Terminology used for acanthodians follows Watson (1937), Denison (1976) and Zidek (1976).

**Morphological research** of previously unknown juvenile individuals of antiarch placoderms *Asterolepis ornata*, as well as juvenile and adult individuals of acanthodian *Lodeacanthus gaujicus* has been done. The development of armour plates and squamation was studied in details.

The methodology of research of the early ontogeny was developed. Quantitatively and qualitatively changeable features characterizing the ontogenetic development of fishes were determined. The determination of the qualitatively changeable characters is based on the quantitatively changeable characters. Consequently the developmental stages of the juveniles of placoderms and acanthodians were proposed.

Morphological features characterizing each developmental stage are reliable characters for distinguishing the developmental sequence of the dermal armour or the squamation of the same species, thus preventing the description of new taxa based on each ontogenetic stage or other misinterpretations in the future.

The qualitatively changing characters developed remarkably rapidly to compare with the quantitatively changing characters: individuals belonging to the subsequent ontogenetic stages exhibit very weak differences in their total length. Such methodology is not useable in the later stages of the ontogenetic development due to no more appearance of the qualitatively changing characters.

Several quantitatively changeable features were selected: 1) body length, body part ratios, proportions of scales, thickness of the armour plates for placoderms; 2) body length, the length of the fin spines, head and body ratio, scale size, fin spine ratio for acanthodians.

Such qualitatively changeable characters were determined: 1) ornamentation of the armour plates, type of sutural connections, presence of the ridge system, histological structure of the armour plates and scales, shape of scales, presence of the sensory line system grooves for placoderms; 2) sequence of ossification of bones, the developmental run of the scale covering for acanthodians. Several ontogenetic stages were proposed depending on the set of quantitatively and qualitatively changeable characters.

Different zones of the scale covering have been described for acanthodians. Acanthodian scales were measured, drawn and described as it is accepted for morphological studies of these fishes (Upeniece, Beznosov, 2002). Thin sections of scales were made by P. Beznosov (Institute of Geology, Komi Scientific Centre, Uralian Division of RAS) for the determination of the scale type.

### 2.4. Methods of taphonomical research and palaeoecological reconstructions

The following methods were used to achieve the results of taphonomic and palaeoecological study. All collected specimens of various taxa were determined and counted to determine the correct number of species, approximate number of individuals and the taxonomical composition of the Lode fossil assemblage. Taphonomical studies included evaluation of preservation state, modes of preservation, spatial distribution, orientation and disarticulation of organism remains. Besides, the correlation between the state of preservation and lithologic type of the sediments was established, thus several types of taphocoenoses were determined and distinguished. The research of the sequence of disintegration of fish bodies significantly added for understanding of the palaeoenvironment of burial in the Devonian deltaic region. Actuopalaeontological method was used for comprehending the different preservation state of fossils in the same taphocoenoses.

Autochthonous or allochthonous character of burial for fishes, invertebrates and plants has been determined whenever it was possible. Morphofunctional analysis of the organisms from the Lode assemblage indicates the lifestyle and habitat of various taxa, allowing reconstruction of the food chains existed during the Lode time. The actuopalaeontological method was used also establishing the food web and trophic levels in ecosystems of the Lode time: producers, primary and secondary consumers, and predators were determined substantiated on the comparison to those in modern trophic pyramids. The habitats of extinct fishes such as placoderms were additionally determined based on the investigations of the thin sections of the stomach content. The quantitative analysis of the exact number of fish individuals from various taxa confirmed their designation to different trophic levels. Number of fishes infested by parasitic helminthes belonging to the two yet undescribed taxa has been counted to evaluate the degree of invasion.

# 3. Palaeoecology and fish taphonomy at the Lode fossil site

## 3.1. Distribution of fossils in the ”juvenile fish” lens

The ”juvenile fish” clay lens represents a clay-filled 66 m wide slump depression, which has yielded unique fossil assemblage containing complete skeletons of juvenile fish individuals, as well as diverse invertebrates and plants (Upeniece, Upenieks, 1992; Upeniece, 1995, 1996, 1999, 2000, 2001b). Various problematic remains occur also.

The almost total absence of a burrowing infauna is characteristic for the lens, differing from that in non-laminated, fine-dispersed yellow-greyish clay lens with adult *Asterolepis ornata* in other parts of the quarry. Only in one case small burrows filled with non-carbonate light material have been observed. Partly the fossils are found as fragments because the laminated clays dry out when exposed and therefore have been broke.

The lens consists of dense, finely dispersed, dark grey clay laminites rich in organic matter (Fig. 3.1.) interbedded within the medium-coarse sandstones. These finely laminated clays are distinctive from the other lenses within the Lode pit; no significant lithological change indicates a steady environment. The delicate lamination is deformed only by abundant coprolites during their deposition into oozes, as well as by clay ”bubbles”, the origin of which will be dealt below. The unusual distribution of deep red clay interlayers (1-3 cm thick) is characteristic for this lens. Randomly distributed siltstone interlayers and spots of sands appear. Abundance of articulated remains in quiet water must be the evidence of anaerobic bottom conditions and rapid burial, which might be the most obvious reasons for excellent preservation.

A detailed geologic section of the ”juvenile fish” clay lens (Fig. 3.1) represents the frequencies of fossils: rare (one or very few) and common finds are distinguished during the excavations of 11 years (1988-1998), carried out by the author. The total thickness of deposits exceeds 12 m, of which 7 m are rich in fossils. The clay unit had been extended over the top of the outcrop for at least 5 m. Central parts of the lens represent deposition in the deepest water with the majority of articulated fish and abundant finds of crustaceans (Upeniece, Upenieks 1992, Fig. 1). The thickness of the beds decreases towards the edge of the clay lens; here incomplete fish skeletons and isolated armour plates, as well as rare little slumps (up to 10 cm) occur. The thickness of the juvenile fish bearing bed (No 40) decreases from 20 cm to 10-12 cm. Siltstone and multicoloured clayey gravel – pebble size rolls with clayey-silt cement occur towards the bottom of the clay lens; content of coarse-grained sediments increases: silty clays, sandstone interlayers, sandy clays and sandstone have been found here (Fig. 3.1). The latter represent the Sietiņi Formation and form the bottom of the slump depression.

The majority of the lens had been already used for the brick production before 1984. Actually only a few percent remained due to the yearly sliding down of the waterlogged clays. This lens now is under protection as one of the Geological and Geomorphological Nature Monuments of Latvia (MK, 2001; Stinkulis, 2003), suggested by the author in 1991 (Latvijas Universitāte, 1991).

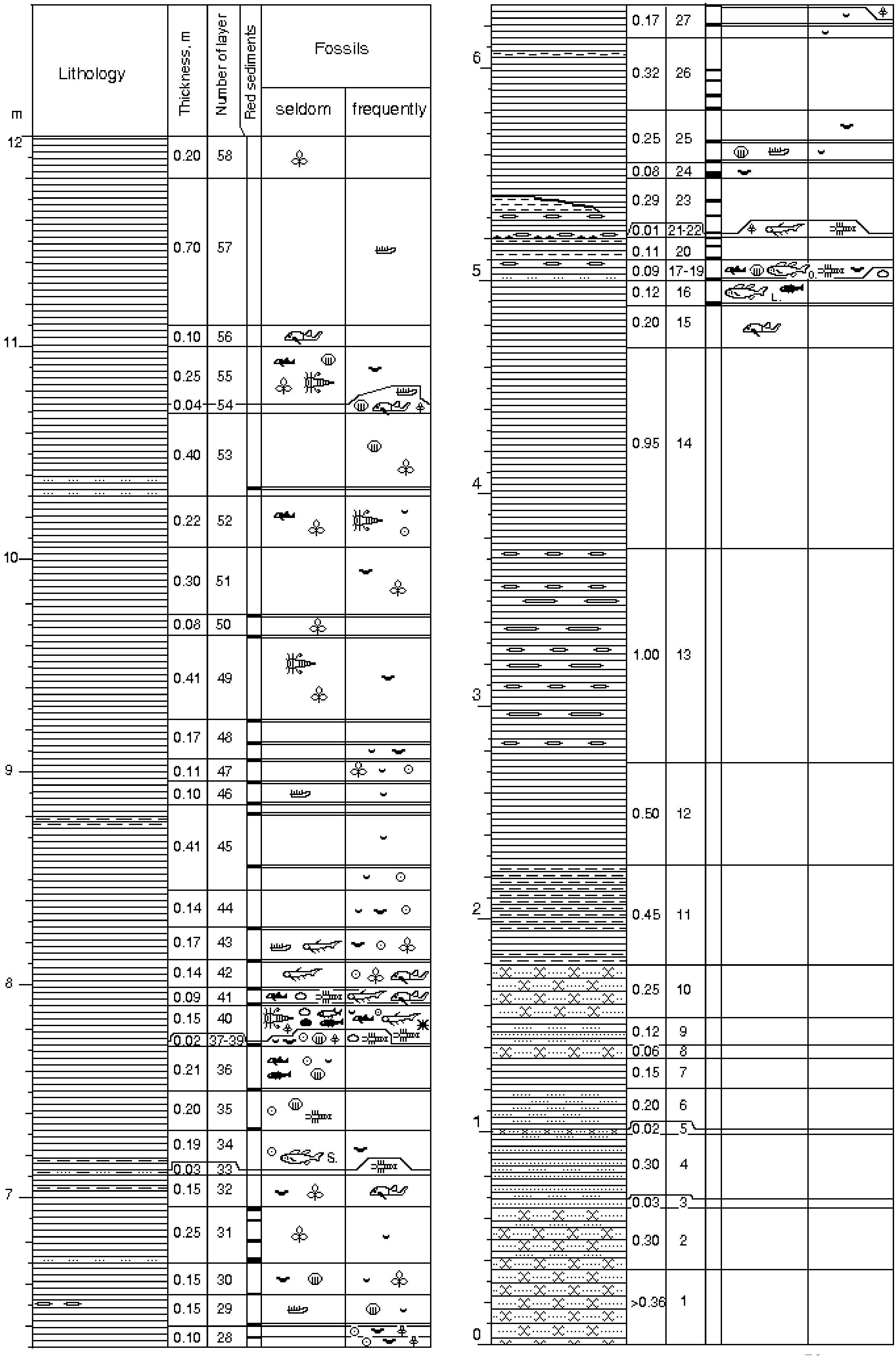

Lithology
Thickness, m
Number of layer
Red sediments
Fossils
seldom
frequently
m
12
11
10
9
8
7
6
5
4
3
2
1
0
0.20 58
0.70 57
0.10 56
0.25 55
0.04 54
0.40 53
0.22 52
0.30 51
0.08 50
0.41 49
0.17 48
0.11 47
0.10 46
0.41 45
0.14 44
0.17 43
0.14 42
0.09 41
0.15 40
0.02 37-39
0.21 36
0.20 35
0.19 34
S.
0.03 33
0.15 32
0.25 31
0.15 30
0.15 29
0.10 28
0.17 27
0.32 26
0.25 25
0.08 24
0.29 23
0.01 21-22
0.11 20
0.09 17-19
0.
0.12 16
L.
0.20 15
0.95 14
1.00 13
0.50 12
0.45 11
0.25 10
0.12 9
0.06 8
0.15 7
0.20 6
0.02 5
0.30 4
0.03 3
0.30 2
>0.36 1

Fig. 3.1. (previous page) Detailed geologic section of ”juvenile fish” lens. Liepa (Lode) clay pit, Devonian, Latvia (Upeniece, 2001 b, Fig. 2).

3.1. att. (iepriekšējā lappaspusē) “Zivju mazuļu” iegulas detalizēts ģeoloģiskais griezums. Liepas (Lodes) māla karjers, devons, Latvija (Upeniece, 2001 b, Fig. 2).

**Abbreviations:**
**Apzīmējumi:**

▤ Fine-dispersed grey clay
Sīkdispersi pelēki māli

Silty clay
Aleirītiski māli

Sandy clay
Smilšaini māli

Siltstone
Aleirolīts

Sandstone
Smilšakmens

Clayey pebbles
Māla oļi

Rough bedding plane
Nelīdzena slāņojuma virsma

**Placoderms Bruņuzivis**
*Asterolepis ornata:*
juveniles, zivju mazuļi
adults, pieauguši īpatņi

**Acanthodians Akantodes**
*Lodeacanthus gaujicus*

**Actinopterygians Starspures**
*Cheirolepis* sp.

**Sarcopterygians**
**Daivspuru zivis**
juveniles of *Strunius* sp.n., *Latvius* sp.n. zivju mazuļi

L. adults of *Strunius* sp. (S.), *Laccognathus panderi* (L.), Osteolepididae (O.) pieauguši īpatņi

Fragments, teeth; fragmenti, zobi
scales, zvīņas

**Merostomata**
**Vēžskorpioni**

**Crustaceans:**
**Vēžveidīgie:**
eumalacostracans, augstākie vēži

○ conchostracans, lapkājvēži
● ostracods, gliemeņvēži

✳ **Parasitic worms**
**Parazītisku tārpu atliekas**

**Plant remains**
**Augu atliekas**

**Coprolites:**
**Koprolīti:**
< 0.5 cm,
0.5-10 cm

⊙ Clay ‘’bubbles’’, māla “burbuļi”

## VERTEBRATES

Vertebrates are represented in this lens by juvenile and adult fish mostly of small size (0.8 - 4 cm). Extremely well-preserved complete skeletons of juvenile individuals of four taxa occur in the lens: *Asterolepis ornata, Lodeacanthus gaujicus, Strunius* sp.nov., and *Latvius* sp. nov. (Upeniece, 1996). The undisturbed scale-cover is preserved in many cases. Seldom fragmentary remains of *Cheirolepis* sp. and Coelacanthidae gen.et sp. indet. are observed. The good preservation of both adult and juvenile specimens of the first three mentioned species provides information on the sequence of certain growth stages.

The overwhelming majority of juvenile *Asterolepis ornata* comes from the layer No. 40. Several adult specimens of *Asterolepis ornata* (without caudal parts) occur at some levels of this lens (Fig. 3.1), but separately from the juvenile fish findings; the length of the dermal armour of adults comprise 30-35 cm. All are poorly preserved as three-dimensional carcasses of powdery composition due to almost complete leaching and low level of mineralization, although ornamentation of the bones is excellently preserved. An adult specimen of *Laccognathus panderi* with total length of the body at least 1.65 m was exposed in the lower part of the lens near the margin of the depression (layer No. 16) (previously excavated fishes reveal 0.8-1.3 m; Lyarskaya, 1981, p.39). This individual is light grey in colour, and not black or brown, so characteristic for the other fossils in this lens. Possibly it might be due to occurence of this fossil near the margin of the depression.

**Juveniles of *Asterolepis ornata.*** These reveal a sequence of growth stages, ranging from initial ossification of the dermal armour to advanced juveniles (Upeniece, Upenieks, 1992). Approximately 95% (more than 300) of specimens are individuals of similar size with the total armour length about 1.5 cm. These could be individuals from one spawn.

The fish bodies are more or less deformed, and often filled with clayey mud sediments which surround the animal. The thickness of sediment fillings reaches 0.1-1.0 mm. It is considerably greater in the adults of *Asterolepis ornata* (up to several cm) where infilling preserves three-dimensionally the animal to some extent. Empty, and therefore more flattened and crashed juvenile specimens also occur.

*Asterolepis ornata* juveniles have been found in close association with small acanthodians and sarcopterygians. The first finds of *Asterolepis ornata* juveniles were made in 1986. The morphology and ontogeny of these placoderm juveniles are described in the fourth chapter.

**Acanthodians.** More than sixty individuals of *Lodeacanthus gaujicus* Upeniece, 1996 were found during regular excavations. They represent both juvenile and adult individuals with body length of 0.8 to 4.8 cm (both estimated). All developmental stages from juveniles without scales to fully scaled specimens are found (Upeniece 1996, Pl.1). One fourth of all specimens are juveniles. The body of the youngest fish fry is covered merely with a film of the skin; the head is indicated only by the presence of an eye stain, and a few branchiostegal rays, with fin spines and scapula confirm that it is an acanthodian (Upeniece, 2001b, Pl. 2 Fig. 10); the length of it comprise about 0.8 cm (LDM 270/45). The next ontogenetic stages include preserved exoskeletal bones and initial stages of the squamation. In detail it will be dealt in the fifth chapter dealing with acanthodians.

**Sarcopterygians.** Several taxa of small sarcopterygians include juveniles and adults of *Strunius* sp. nov. (Upeniece, 1995), juveniles of *Latvius* sp. nov., as well as fragments of adults of Osteolepididae gen. et sp. indet. Juveniles of *Strunius* sp. nov. are up to 2 cm long. They lack the harpoon-shaped sigmoid tooth tips which characterise the adults. The length of adult individuals is estimated to be at least 12 cm. Several bones of the adult reveal peculiar ornamentation. In addition, the scale cover and fragment of the anal and caudal fins of one juvenile coelacanth was found in 1994 (identified by Prof. H.-P. Schultze 1999 in Riga; Upeniece, 2001b).

**Actinopterygians.** Fragments of the actinopterygian *Cheirolepis* sp. have also been found: 1) several detached head bones and scale cover; and 2) fragment of fin and scale cover. Minute scales and small fin rays suggest they could belong to juvenile individuals. To compare with the size of *Cheirolepis canadensis* from Miguasha (Schultze & Cloutier, 1996, Fig. 3A) and of *Cheirolepis trailli* from Scotland (Trewin 1986, Fig. 22) the *Cheirolepis* sp. from Lode probably represents juvenile indivuduals.

## INVERTEBRATES

**Parasitic worms**. Circlets of previously unknown fossil hooks (Figs. 3.2., 3.3., 3.4., 3.5.) were found in 16 juveniles of *Asterolepis ornata* and in 27 specimens of *Lodeacanthus gaujicus* during study of morphology. The length of the hooks is 0.02-0.40 mm. They are located in the gill regions, near the fin spines, and in the abdominal region of acanthodians. The hooks must be remnants of parasitic organisms due to their specific location (Fig. 3.4. B) and occurrences in different fishes (Upeniece, 1999 a,b,c). That specific location indicates they presumable belonging to representatives of ectoparasites and endoparasites. Small sized acanthodians possessed small sized hook systems of parasitic helminthes; larger acanthodians exhibit the greatest in size hook systems. Hence, parasites might have spent all their life in a one host. In asterolepids the location of the hooks is not so determined. The length of infested fishes reaches 1-4 cm. Several of them were infested with two to nine parasites (Fig. 3.2. A).

Altogether the remains of 77 parasitic worms were found. Two of them were found in one individual of crustacean Mysidacea (the hooks seems to be too large for parasitism judging from the size of the crustacean), and one close to a specimen of Conchostraca.

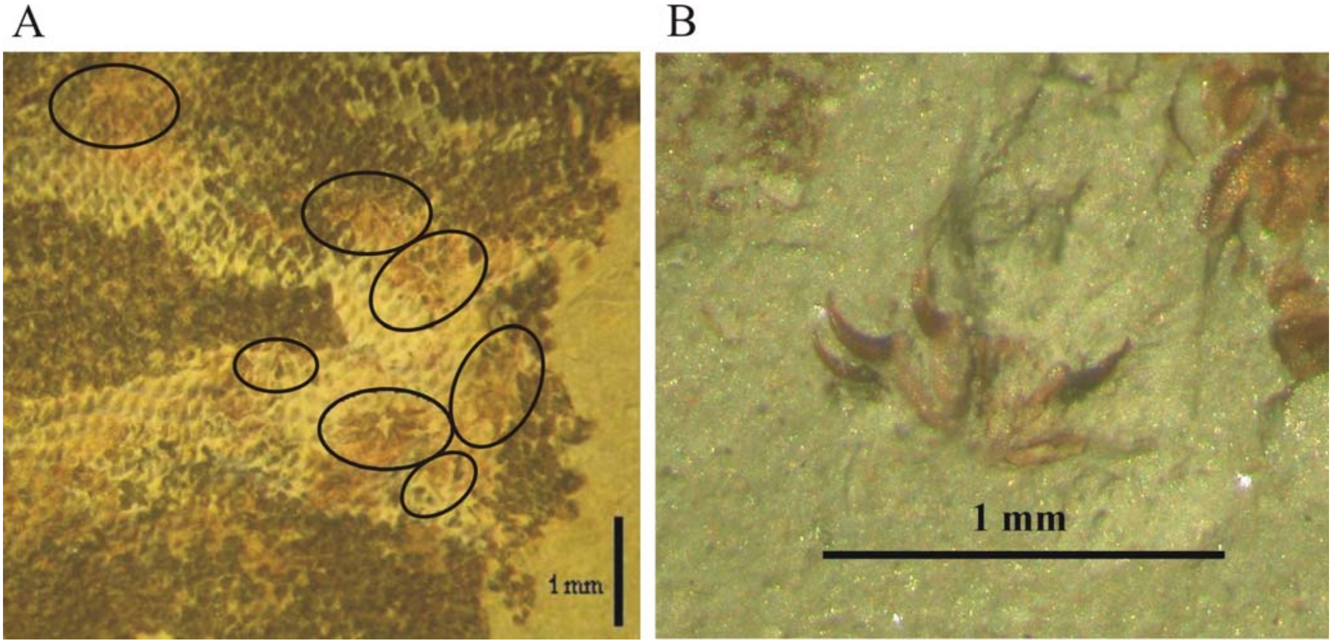


Fig. 3.2. Fossil circlets of parasitic platyhelminths hooks (marked with ellipses in A) inside the acanthodian *Lodeacanthus gaujicus*. A, LDM 270/18c (Upeniece, 2001b, Pl. 3, fig. 2); B, LDM 270/33a. Upper Devonian, Liepa (Lode) pit.

3.2. att. Fosilo parazītisko plakantārpu piestiprināšanās kāsīši (A attēlā - apvilkti ar elipsēm) akantodēs *Lodeacanthus gaujicus*. A, LDM 270/18c (Upeniece, 2001b, Pl. 3, fig. 2); B, LDM 270/33a. Augšdevons, Liepas (Lodes) karjers.

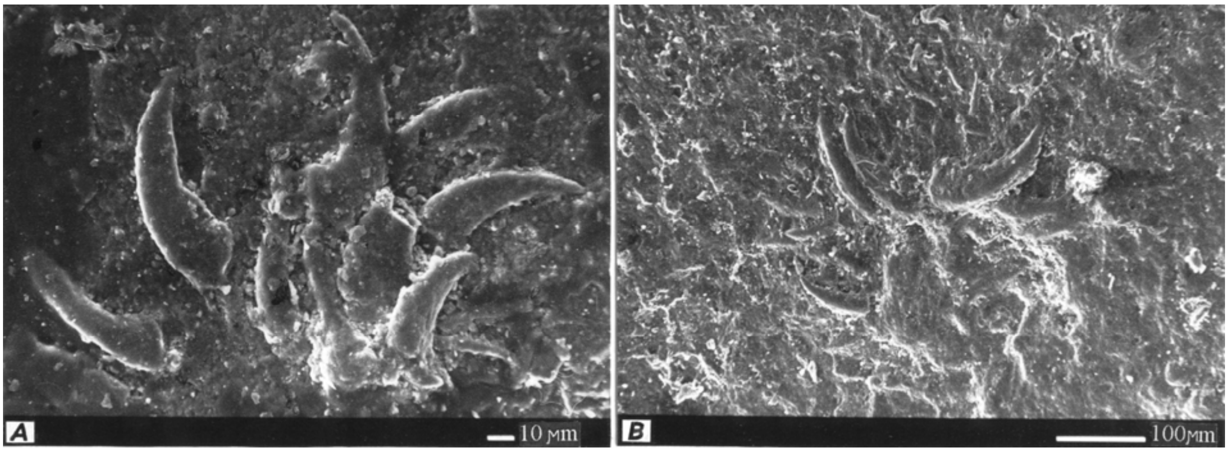


Fig. 3.3. Fossil hooks of parasitic platyhelminths. **A,** found in juvenile acanthodian body near the scapula (see also Fig. 3.5. No 17), LDM 270/4a. **B,** found near conchostracan. Upper Devonian, Liepa (Lode) pit.

3.3. att. Fosilo parazītisko plakantārpu piestiprināšanās kāsīši. A, atrasts akantodes mazulī pie lāpstiņas kaula (sk. arī Fig. 3.5. Nr. 17), LDM 270/4a. **B,** atrasts pie lapkājvēzīša. Augšdevons, Liepas (Lodes) karjers.

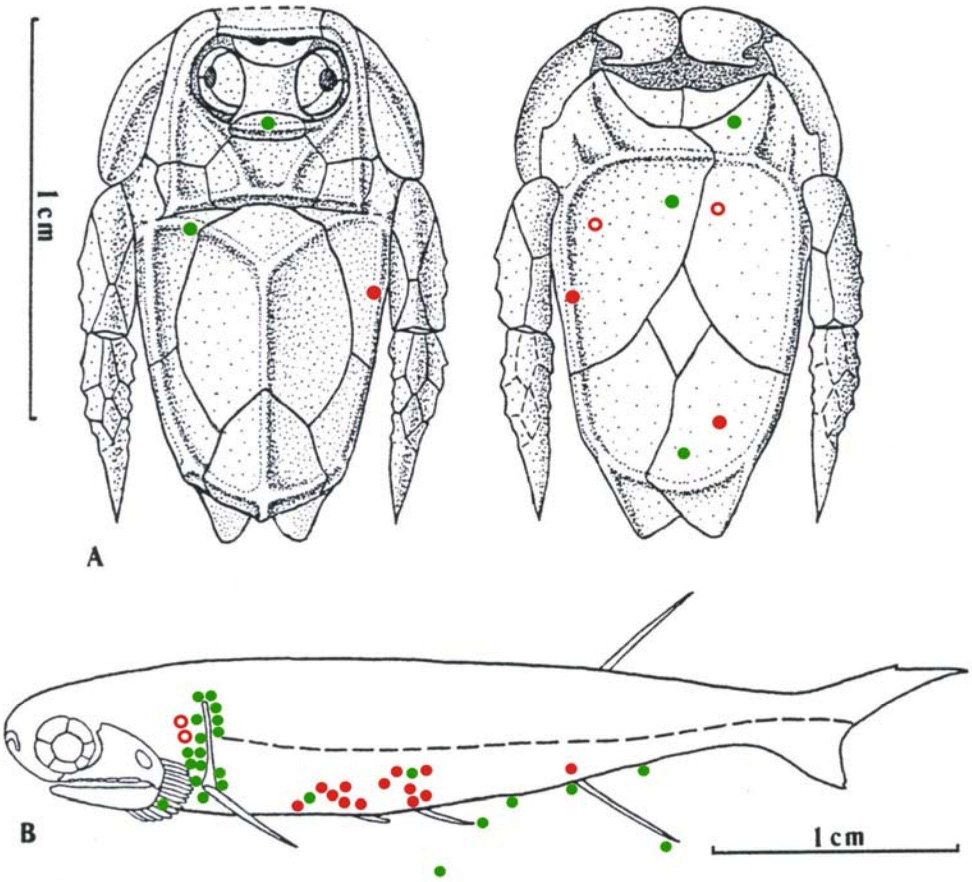


Fig. 3.4. Localization areas of remains of parasitic platyhelminths. **A,** in placoderm juveniles of *Asterolepis ornata*. **B,** in juvenile and adult acanthodian *Lodeacanthus gaujicus*. Red circles – possible endoparasites, green circles – possible ectoparasites.

3.4. att. Parazītisko plakantārpu lokalizācijas vietas: **A,** bruņuzivju *Asterolepis ornata* mazuļos. **B,** akantožu *Lodeacanthus gaujicus* mazuļos un pieaugušos īpatņos. Sarkanie aplīši – iespējamie endoparazīti, zaļie aplīši – iespējamie ektoparazīti.

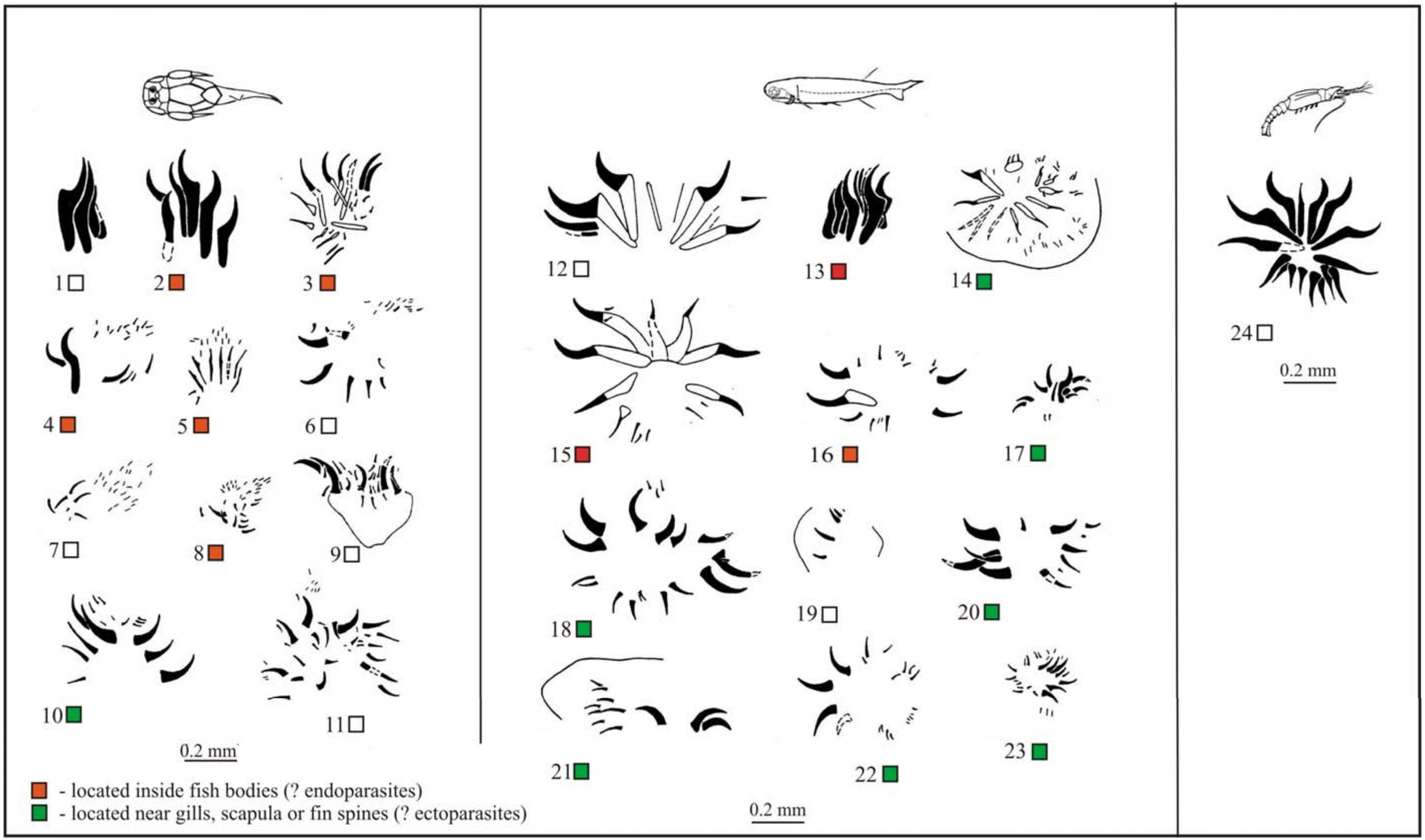


Fig. 3.5. Circlets of fossil hooks found in juveniles of placoderm fish *Asterolepis ornate* (No 1-11), in juveniles and adults of acanthodian *Lodeacanthus gaujicus* (No 12-23), and in/on crustacean Mysidacea (No 24) (Upeniece, 1999 a, Fig. 1).

3.5. att. Fosilo parazītisko tārpu atlieku – kāsīšu atradumi bruņuzivju *Asterolepis ornata* mazuļu skeletos (Nr. 1-11), akantožu *Lodeacanthus gaujicus* mazuļu un pieaugušu īpatņu skeletos (Nr. 12-23), kā arī vienā šķeltkājvēzītī Mysidacea (Nr. 24) (Upeniece, 1999 a, 1.att.).

Recent parasites possessing such hooks are known within the two phyla Platyhelminthes and Acathocephala; hooks are used as the attachment organ to the host (Fig. 3.6.). The circular arrangement of the bilaterally symmetrically located hooks and traces of cuticular disc indicate that these examples could belong to the platyhelminth superclass Cercomeromorphae Bychowsky, 1957 (Schultz, Gvozdev, 1972), where larvae have radialy arranged chitinous hooks for attachment. The size of the fossil hooks is about ten times larger than those in the modern Cercomeromorphae. Some hook systems may have resemblance of that with the members of the phylum Acanthocephala. The absence of modern analogues points to the extinct group of parasites.

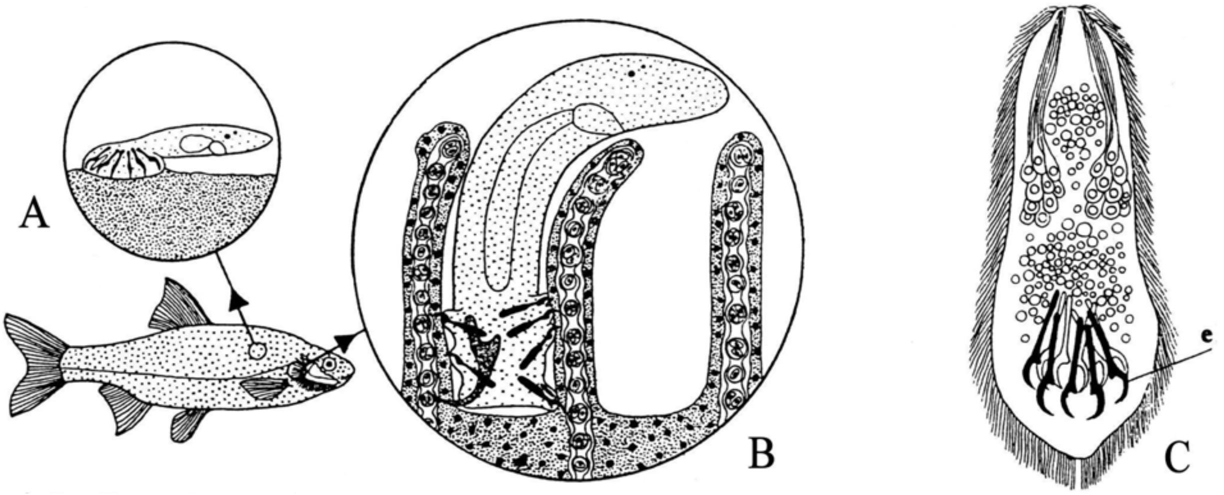


Fig. 3.6. Recent parasitic flatworms. **A,B,** *Neodactylogyrus crucifera* (Monogenoidea) life style (Kearn, 1968, fig. 17): **A,** the early skin-parasitic larva. **B,** the gill-parasitic adult on the host (roach). C, larva of *Gyrocotyle urna*; e – embrional hooks (Ruszkowski, 1932).

3.6. att. Mūsdienu parazītiskie plakantārpi. **A, B,** *Neodactylogyrus crucifera* (Monogenoidea) dzīves veids (Kearn, 1968): **A,** kāpurs uz zvīņojuma. **B,** pieaudzis parazīts starp raudas žaunu lapiņām. **C,** *Gyrocotyle urna* kāpurs; e – embrionālie kāši (Ruszkowski, 1932).

No fossilised soft body parts were found, except traces of the disc outline. Diagnostic soft parts of parasitic helminths are absent. Different morphological groups of the hooks are presented in both species of fish. The hooks are of two types: with a handle and without it. The hooks with handles occur in the abdominal region of acanthodians and placoderms, suggesting that they belonged to endoparasites (Upeniece, 2001b, Pl.3, Fig. 2).

The discovery of parasitic remains in Devonian fish fossils confirmed the hypothesis of Llewellyn (1982) on phylogeny of parasitic flatworms in fishes. These remains could have represented ancestors of flatworms Monogenea. The maximum number of the hooks 16 evidenced that. It is characteristic to primitive monogeneans (Boeger, Kritsky, 1993).

No fossil parasitic Platyhelminthes have ever been described (Conway, 1981; Grey, 1988). With the exception of some eggs and larvae recorded from archaeological sites (Gooch, 1975) the fossil record of parasitic Platyhelminthes is non-existent (Conway, 1981). The only other known fossil flatworms are Miocene turbellarians from California (Pierce, 1960), but they are free-living taxa. Two Vendian genera were described from White Sea bank, but their belonging to the phylum Platyhelminthes, as turbellarians, is proposed to be confirmed (Fedonkin, 1985, p.90). So far nothing about fossil parasitic flatworms is known (Grey, 1988; Poinar, 2003).

The fossil record of fish parasites is rather poor, with one record in the Palaeozoic, and one in the Mesozoic. Zangerl, Case (1976) have described countless tiny fossil ellipsoidal bodies from the coprolitic rectal fill of Pennsylvanian shark *Cobelodus aculeatus* (Cope), which they interpreted as a mass of helminth eggs, perhaps of cestode origin. Well-preserved Lower Cretaceous fossil parasitic copepods were described from the gill chambers of two skulls of the teleost fish *Cladocyclus gardneri* Agassiz from Brazil (Cressey, Patterson, 1973).

Parasitic platyhelminth remains recorded in the juvenile fish bodies from Lode, Latvia represent the oldest fossil record of fish parasites (Poinar, 2003, Table 1), as well as the oldest parasitic association ever found (Boucot 1990, Tables 4,6,7,9).

**Crustaceans.** Thousands of well-preserved crustaceans belonging to the order **Mysidacea** (class Malacostraca, subclass Eumalacostraca, superorder Peracarida) where found in this lens by Mr. Jānis Upenieks in 1984, representing the richest accumulations of eumalacostracans in the Devonian (Upenieks, 1990). The Eumalacostraca are known from seven Devonian localities from Euramerica, five of them from Europe (Schram, 1977). Devonian malacostracan material is rare and usually poorly preserved (Schram, 1980).

Complete specimens with eyes, uropods and two pairs of antennae are preserved in the material from Lode (Upeniece, 2001, Pl. 2, Fig. 1). In some cases the stomach and intestine content occurs as a brown powdery mass with carbonised remains. The mysidaceans must have served as fish food. Most mysidaceans are 1 cm long, but small, 0.5 cm long specimens also occur. Almost all specimens are located in upside-down position on the bedding plane randomly orientated, implying post-mortem transportation. Several separately found individuals reach the length of 1.5 cm. The body of mysidians from Lode resembles that of the mold of a lost and undescribed specimen from the borehole at Kaluga, near Moscow, Upper Devonian (Schram, 1980, Pl. 1, Fig. 3).

Four layers with abundant and dense concentration (three to five specimens/cm$^2$) of whole-bodied mysidaceans occur in this lens. Spotty accumulations of them occur close to the margin of the clay filled depression.

In two layers (No. 22 and 33, Fig. 3.1) they are restricted to a 1-1.5 cm thick silt/sandstone interlayer, where accumulations in several bedding planes occur. The preservation of their carapaces varies: in layer No. 22 mysidaceans are white in colour, carapaces react with HCl, without any traces of chitin covering (completely leached chitin could have been substituted with carbonate); in the layer No. 33 the chitin covering is completely preserved (Upeniece, 2001, Pl. 2, Fig. 1). Two levels with mysidaceans are restricted to clay (No. 19, 39); the chitin is nearly translucent and is thought to be the result of moulting.

**Conchostracans** are common fossils within a narrow zone of reddish-brown fine-dispersed clay within the layer No. 37. They form a taphocoenosis together with the alga *Platyphyllum* sp. Shells are translucent; usually both valves are preserved, and their length is up to 1cm. They occur also irregularly within layers containing juveniles of *Asterolepis*. Some conchostracans are identified as *Pseudestheria* sp. (Upeniece, 2001, Pl. 2, Fig. 9) by their concentric growth lines and characteristic reticular microornamentation between lines. At least three new taxa of conchostracans may be present in the material.

**Ostracods** are preserved only as moulds of 0.3-1.3 mm in length. They are oval and smooth and no specific morphological features can be observed. Commonly the moulds of both valves are present; sometimes they are in open position. Their shell might have been a very thin structure. Ostracods are found near the juveniles of *Asterolepis ornata* as well as on the separate bedding plane of variegated clays (Upeniece, 2001, Pl. 2, Figs. 6, 7).

Many crustacean remains are undeterminable.

**Eurypterids.** Eurypterids (Merostomata) occur only as fragmental material, but are readily identified by their specific semilunar ornamentation on the segments (Upeniece, 2001, Pl. 3, Fig. 3). The carbonate material is completely leached, and only chitin is preserved. These are the first finds of eurypterids in the Gauja Regional Stage, and they belong to a new taxon. Both adult and juvenile specimens are recorded. The adults are estimated to be about 1m in length, exceeding those found in the deposits of the Salaspils and Pļaviņas regional stages of the lower Frasnian, Latvia. Eurypterids are known to be inhabitants of brackish waters; they may have been feeding on smaller invertebrates.

## PROBLEMATIC REMAINS

**Problematic** soft-bodied and phosphatic remains are common. Unfortunately, it is not possible to identify their taxonomic position (Upeniece, 2001, Pl. 1, Fig. 5). Several egg-like structures (ibid, Pl. 2, Fig. 2-5) could belong to invertebrates, judging by their small size. Separate "eggs'' also are collected; they reveal the peculiar pit on the surface (blastula?).

**Clay ”bubbles”** are abundant throughout the clay lens. They are interpreted to have originated due to decomposition gases enclosed in the sediment around decaying soft-bodied organisms (Upeniece, 2001). These resulted in concentric circles above and below the assumed organisms or their remains (Upeniece, 2001, Pl.3, Fig. 4). Evidence supporting this is the fact that many bubbles contain coprolites of various sizes. As the organic part of the coprolite decayed, gas was formed, and a bubble-like clay structure was produced. The linear-shaped coprolites produce clay ''bubbles'' of oval shape. In one case, evidence of the gas escaping process was observed in the middle part of the ventral wall of an adult *Asterolepis ornata*, with a clay bubble approximately 4 cm in diameter lying between the margins of MV and PVL plates.

## COPROFOSSILS

**Coprolites.** Coprolites are exceedingly abundant throughout the section (Fig. 3.1.). They vary in shape and in structure, and are derived from both carnivores and herbivores. Coprolites of herbivorous animals contain carbonised plant fragments. Several scroll coprolites (Upeniece, 2001, Pl. 3, Fig. 7, 8) contain bony material, acanthodian scales and spines, and small scales of sarcopterygians (*Latvius* sp. nov., *Strunius* sp. nov.). The material is present both on the surface and in the interior of the coprolites. Some coprolites contain twisted parts of acanthodian bodies, making it obvious that their spines did not prevent ingestion of the whole animal. The spines of acanthodians are normally rare in coprolites (McAllister, 1989, 1996, p. 344; Trewin, Davidson 1996, Fig. 8a).

## TRACE FOSSILS

**Ichnofossils.** Ichnofossils are almost absent in the ”juvenile fish'' lens, but there are a few samples with horizontal traces (?).

**PLANTS**

Plants are represented by possible algae *Platyphyllum* sp. (Upeniece, 2001, Pl.4, Fig.4), and Progymnospermopsida by *Svalbardia polymorpha* Høeg, 1942 (*ibid*.: Pl.4, Fig. 2,3,5) and *Archaeopteris fissilis* Schmalhausen (*ibid*.: Pl. 4, Fig. 1). *Svalbardia* and *Archaeopteris* could be synonyms (Meyen, 1987, p.136). Megaspores presumably belonging to *Archaeopteris*, which resemble those in Meyen (1987, Fig. 35 f), have been found near and on the juveniles of *A. ornata*.

An oogonium of the charophyte *Trochiliscus* sp. has been found in the stomach content of an *A. ornata* juvenile during the preparation of thin sections. Two finds of Charophyta gen. et sp. indet. with left coil could belong to Charales (Upeniece, 2001, Pl. 4, Fig.6).

## 3.2. Fish taphonomy

Fish taphonomy may contribute information about the depositional environment, paleocommunity, mortality and preservation. Taphonomic reconstruction of ecology and preservation depends on the applicability of analogous processes in modern ecology and sedimentology.

All remains of organisms in the "juvenile fish" lens are black or brown in colour. It is contrary to the findings of the whole-bodied adults of asterolepids and sarcopterygians, found in the yellow-greyish clay in the same quarry; where fish fossils are white or light-coloured.

Rather extensive material of placoderm *Asterolepis ornata* remains together with sedimentological and taphonomical features allows study of the sequence of body disintegration (Upeniece, 1999) and understanding of the influence of palaeoecological factors on the formation of several types of taphocenoses (Upeniece, 1991, Kuršs *et al*. 1999). There is an orderly sequence of decomposition degrees from essentially perfect articulation to total disarticulation, established during several excavations of *Asterolepis ornata* fish-bearing beds in the Lode clay quarry (Table 3.1) outside the "juvenile fish" lens.

### 3.2.1. Disintegration process of placoderm *Asterolepis ornata* body

Some 35 bodies of adult placoderm fishes *Asterolepis ornata*, disintegrated to different degrees, were exposed on area approximately of 16 m$^2$ in 1988 field season (Fig. 3.3), giving the possibility to study the disarticulation process (Upeniece, 1999). Several skeletons of *Laccognathus panderi* (damaged by excavator), as well as some plates of *Psammolepis alata* were also exposed in this bed. Fish skeletons were covered by 15-25 cm thick laminae of light grey-yellowish finely-dispersed and silty clay with abundant vertical burrows, as well as conchostracans. Thin, only 1 cm thick layer of bluish-grey clay occurs immediately below the fish-bearing bed, containing abundant accumulations of *Laccognathus panderi* scales. The basal part of the rhythmic sequence consists of a 0.3 cm thick sandstone layer. The thin sandstone layer in thickness of 1 cm occurs above the fish-bearing clay layer.

All remains were laid on the same level excluding a large account of *Asterolepis ornata* scales and *Laccognathus panderi* teeth which were scattered into the whole bed; scarcely remains of conchostracans occur. All placoderm skeletons were retained in the three-dimensional state, although due to the compression of clay beds the armour plates were folded over one another. Dorsal sides were always turned upside top; separate plates with the convex surface up show stable position, which is typical for an active hydrodinamic environment.

The jaw elements and those bones, which are situated within the orbital fenestra (sclerotic bones, nasal and pineal plates), were connected to the skull roof by soft tissues forming the slightly movable and fully movable synovial or cartilaginous joints, hence these skeletal elements were readily disconnected from the rest of the body in the very first stages of disintegration due to weak currents (Table 3.1., disintegration stages 1, 2). Fully articulated fish skeletons suggest burial in the deep water or in the local deep depression where rapid sedimentation took place. Most probably these fishes were buried alive or very fast after death, and were not subjected even to the weak or gentle currents.

Only four placoderm skeletons among the above mentioned 35 ones found within the bed under description demonstrate the state of relatively full articulation, except the jaw and orbital bones. One particular feature is characteristic of this taphocoenoses/tanathocoenosis: the anterior medial dorsal plate (AMD) in 12 cases out of 30 was removed and in 7 cases lay in an upside-down position posteriorly on the body (in Fig. 3.7. the visceral surfaces of those plates are marked with longitudional lines instead of dots). The reason for the above mentioned peculiarity seems to be the internal pressure of decomposition gases in decaying armoured bodies, which pushed out the AMD (Upeniece, 1999, 2001b). This indicates that the fish bodies must not have undergone post-mortem floatation (Table 3.1., disintegration stage 3).

Actuopaleontological investigations show that in cold waters below about $16^0$C, most carcasses do not float but remain on the bottom until buried; some scavenging activity may occur (Elder, Smith, 1988). Evidently, *Asterolepis ornata* bodies were transported into deep waters where the carcasses were prevented from floating due to limited bacterial metabolism and pressure, which suppressed gas bubbles. Small vertical burrows, observed exactly under the fish-bearing bed in this taphocoenosis, indicate some level of oxygen as well as rapid sedimentation of mud.

Subsequently the caudal region and the head (Table 3.1., the same disintegration stage 3) became detached because of easy access for bacteria to the soft tissue. The next stage, partial disintegration of skeletons, is the result of floatation in warm waters (Elder, Smith, 1988). The disarticulation occured while carcass lay exposed on the substrate and resulted from eruption of decomposition gas bubbles (Elder, Smith, 1988). Individuals with partially disarticulated plates show a short distance from the point of origin.

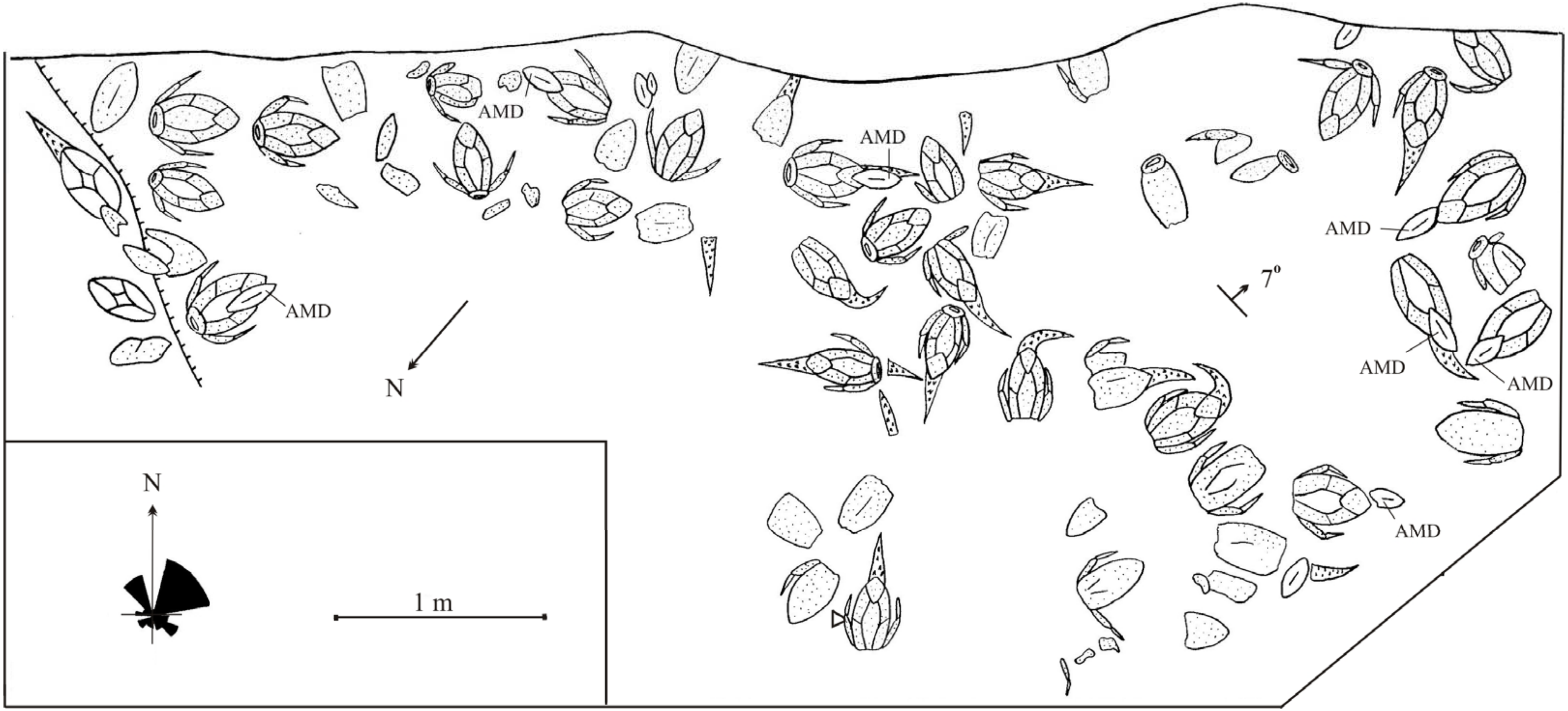


Fig. 3.7. Distribution of adult placoderm *Asterolepis ornata* individuals in one of the largest accumulations in the Liepa (Lode) clay pit. Bodies without dotted central part indicate the pulled out AMD plates (presumably due to the internal pressure of decomposition gases in decaying armour) (Upeniece, 1999, Fig.1).

3.7. att. Pieaugušo bruņuzivju *Asterolepis ornata* izvietojums vienā no lielākajiem to sakopojumiem LIepas (Lodes) mālu karjerā. Brunuzivju ķermeņiem, kuriem ķermeņa centrālā daļa ir attēlota bez punktējuma, ir atdalījušās priekšējās muguras bruņu plātnes (AMD), domājams, trūdgāzu izdalīšanās rezultātā (Upeniece, 1999, Fig.1).

During transportation, weakly connected elements sink first, followed shortly by the deflated body. This resulted in scattering of separate elements and trunk parts over a wide area (Huber, 1992). Therefore the above-mentioned tanathocoenosis must have contained both: 1) articulated, unfloated skeletons (indicated by removed AMD), and 2) disarticulated, previously floated ones (Upeniece, 1999). The displacement of plates and squamous parts might be influenced by weak bottom currents to give the *Asterolepis* skeletons a slight tendency toward a submeridional orientation (Fig. 3.7).

The rate of the loss of body parts from floating carcasses and the state of preservation depending on hydrodynamic activity correlate with the lithology of siliciclastic deposits. The decomposition degree also correlates with the latter. The next recorded stage of disintegration in the sequence, the disconnection of the anterior part of the trunk from its posterior one, have been found in red siltstones (Table 3.1., disintegration stage 4). It is a rarely seen stage of disarticulation. The disintegration stage 5 corresponding to the disconnection of PMD plate from the posterior part of the trunk, is theoretical, not observed within the material.

More frequently, isolated skeletal parts of the trunk-shield (ADL + both AVL, ADL + AVL, AVL + pectoral fin, MxL + PVL, both PVL, both AVL) have been found in the fine-grained greyish-blue sandstone/siltstone as well as in the red siltstone (disintegration stage 6). Sinarthodial fibrous joints between these plates often hold the individual bones together long after the death of the vertebrate, especially the connections between both PVL and both AVL. Obviously, these synarthroses were one of the firmed ones. Subsequent disintegration stages in greyey-blue small-grained sandstones characteristic for the fourth and the fifth type of the taphocoenoses revealed (Table 3.2): separated AVL and PVL (disintegration stage 7); the disconnections of the pectoral fin from the AVL plate (disintegration stage 8) and the proximal segment from the distal one (disintegration stage 9).

Finally, only isolated trunk and head-shield plates frequently occur on a number of bedding planes of the same deposits (disintegration stages 9-10). As it is seen from museums` collections the most durable are plates of the pectoral fin, the lateral plate of the head shield, the processus brachialis element of the AVL, as well as the fragments of the well-thickened ridge system of the trunk armour. The more intensive abrasion, as well as scattering of remains, correlates with coarse-grained sediments as deposited in the most rapid streams and displays the disintegration stages 11 and 12.

The sequence of disintegration of *Asterolepis ornata* juveniles differs a little. The decomposition gas bubbles erupted from the ventral fenestra. In older juveniles with the well-developed MV, the pushed-off AMD has been found, similar to what is observed in adults and has to be described above.

In juveniles some disconnections occurred in earlier disintegration stages than in adults: 1) pectoral fin disconnected from the AVL plate, 2) proximal segment disconnected from the distal one. This could have been due to the more flexible connections to compare with that in the adult individuals.

Table 3.1. Disintegration stages of skeleton of adult placoderm *Asterolepis ornata* of various types of taphocoenoses in the Liepa (Lode) pit

3.1. tabula. Pieaugušas bruņuzivs *Asterolepis ornata* skeleta sadalīšanās stadijas dažādos tafocenožu tipos Liepas (Lodes) karjerā.

| Disintegration stage | Sequence of disintegration | Type of taphocoenosis | Deposits / bedding structure | Probable hydrodynamic environment |
|---|---|---|---|---|
| 0 | Whole skeleton | 1,<br>2 | fine-dispersed grey clays with planar bedding structure | very weak current |
| 1 | Disconnection of jaw elements | 2 | fine-dispersed grey clays | weak and gentle current |
| 2 | Disconnection of orbital bones | 2 | --“-- | --“-- |
| 3 | Simultaneous disconnection of head, caudal part and AMD plate (Fig. 3.3) | 3 | --“-- | gentle current |
| 4 | Disconnection of the anterior part of the trunk from the posterior one | 4 | Red/greyish blue siltstones with indistinct planar bedding | gentle and moderately rapid current |
| 5* | Disconnection of PMD plate from the posterior part of the trunk | 4 | --“-- | --“-- |
| 6 | Disconnection of: 1)MxL from PVL; 2) ADL from AVL;<br>3) plates from the head armour | 4 | --“-- | moderately rapid current |
| 7 | Disconnection of right PVL from the left, right AVL from the left | 5 | cross-stratified and ripple-laminated fine-grained greyish-blue sandstones | --“-- |
| 8 | Disconnection of pectoral fin from the AVL plate | 5 | --“-- | --“-- |
| 9 | Disconnection of separate plates from the pectoral fin | 5 | --“-- | --“-- |
| 10 | Disconnection of separate plates from the proximal segment of the pectoral fin | 5 | --“-- | --“-- |
| 11 | Disintegration of separate plates | 6 | Coarse-grained sandstones | rapid current |
| 12 | Rounding off fragments | 7 | Coarse-grained sandstones, lenses of conglomerates | --“-- |

* - theoretical stage of disintegration (not observed).

### 3.2.2. Disintegration process in other antiarchan fishes

A brief comparison of the above described sequence to that in *Bothriolepis canadensis* has been made. Ten disarticulated individuals were available for that purpose in Stockholm Museum of Natural History, observed by the author in 1998 (Fig. 3.8.). As a whole the sequences of disintegration of asterolepids and bothriolepids are similar. Distinctions are of a morphological nature, as could be expected. The AMD plate is pushed off the armoured body of *Bothriolepis canadensis*, displacing the surrounding bones from the point of origin (Fig. 3.8.). This displacement might be explained by the greater overlapped area of the AMD of bothriolepids. The jaw bones are still preserved, obviously due to their considerably differing morphology. Then the head-shield was detached. After that, isolated skeletal parts, as in asterolepids, occur: ADL + AVL, MxL + PVL. Such state of articulations have been reported also in some other bothriolepids: both AVL plates in *B. gippslandiensis* (Long, Werdelin, 1986, fig. 9), MxL + PVL in *B. kohni* (Young, 1988, p. 49), ADL + AVL in *B. ciecere* (Lukševičs, 1991).

The degree of disintegration correlates with lithology as indicated before. Articulated specimens of *Bothriolepis canadensis* are embedded in flat shaly nodules of limestone. Detached plates occur in a matrix consisting of sandstone rich in carbonates. Fragments of bones are found in a conglomerate.

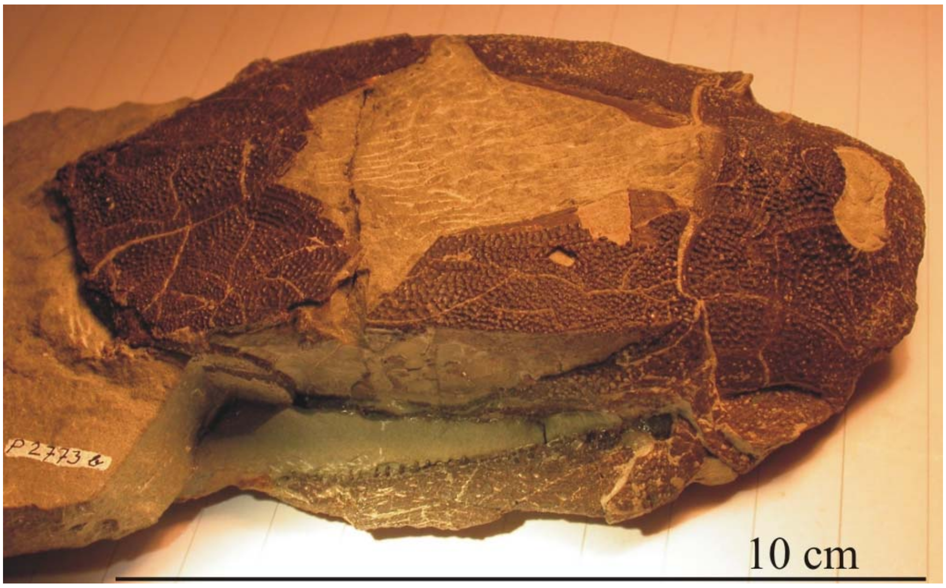


Fig. 3.8. Disarticulated skeleton of placoderm antiarch *Bothriolepis canadensis*. Head and trunk armour. AMD is absent and pulled off due to decomposition gases, specimen P2773b, dorsal side. Upper Devonian, Canada, Miguasha, Scaumenac Bay; haused in Stockholm Museum of Natural History.

3.8. att. Bruņuzivs *Bothriolepis canadensis* daļēji saglabājies skelets. Galvas vairogs un rumpja bruņas ar ķermeņa trūdgāzu izdalīšanās rezultātā atrautu un klāt neesošu priekšējo vidējo muguras plātni (AMD); paraugs P2773b, dorsālā puse. Augšdevons, Kanāda, Miguaša. Stokholmas Dabas vēstures muzejs.

### 3.2.3. Taphonomy of acanthodian *Lodeacanthus gaujicus*

Disintegration process of acanthodian body is completely different as it has different morphology and belongs to the other class. First of all the head became detached, then the scale covering disintegrates. Juveniles with undeveloped scale covering are preserved in dorso-ventral position. The position of body parts sometimes are different in juveniles with partly developed scale covering: the unscaled head in dorso-ventral position, the scaled trunk in lateral position. The lateral position is characteristic for fully or mostly scaled acanthodian individuals. Most of acanthodians are preserved in more or less curved position. In two cases individuals are preserved with opened jaws (LDM 270/5, 270/18), and 15 with closed jaws. A few acanthodian individuals reveal a brown coprolitic-like material in the intestine region.

### 3.2.4. Discussion on fish taphonomy

The early hypothesis, that the Lode taphocoenosis was formed as a result of the catastrophic mass mortality event, was based on their occurrences in the upper parts of the rhythmic sedimentary sequence in grey dispersed clay layers (Kuršs, Lyarskaya 1973; Lyarskaya 1981). It seemed that the mortality was caused by the change of the basin regime. Later the cause was re-evaluated and attributed to the hydrodynamic regime of sedimentation: in basin bottom deeps fish cadavers were accumulated as a result of sorting of organic remains by weak currents. Towards to the borders of these depressions a great number of separate bones accumulated. The colour of clay changed from greenish-grey to variegated and, further, to red (Kuršs, 1986, 1992 b, text-fig. 3).

The same conclusion was applied after the taphonomical research of juveniles of *Asterolepis ornata*, found in the "juvenile fish" lens (Upeniece, Upenieks 1992, text-fig. 1), as well as on their adults, studying the sequence of the disintegration stages, and mentioned above. Obviously these fishes were not killed by one event, but represent accumulation of unfloated cadavers and floated ones, as described above. Fish cadavers were accumulated in a local depression (Kuršs 1992 a, fig. 34) with some influence of weak submeridional currents from north to south (Fig. 3.7.). The occurrence of fish juveniles together with large sarcopterygians scales might imply to similar hydrodynamical flow. Seemingly, the deposition of remains in longitudinal slump depressions depends on similar circumstances as in fluvial channels (Behrensmayer, 1988).

After the death fish carcasses tend to float for a while, then sink to the muddy sea floor, and may be scavenged upon at any time during this period. Thus, the remains of fishes found in the fine dispersed clay (rarely also in siltstone) at Lode comprise complete skeletons, isolated bones or pieces of a carcass. The fish cadavers were rapidly encased in a fine mud, thus protecting the delicate skeletons from being disintegrated.

The placoderms from the first excavation in 70-ies (carried out by Lyarskaya) were dominated a number of times over sarcopterygians. The fish cadavers were deposited in a clay lens (thickness 3 m) in three fish-bearing beds within the area of 5 x 20 m (Lyarskaya, Mark-Kurik, 1972). Fifty-eight individuals of adult *Asterolepis ornata*, four of *Laccognathus panderi*, and one of *Panderichthys rhombolepis* were found in the lower and richest fish-bearing bed of the lens. In the second bed the asterolepids comprise only 25%; in the third domination of asterolepids is shown again (exact number is not stated for these two layers), and sarcopterygians occur only as incomplete specimens. The skeletons of asterolepids are slightly deformed and often found in a position with their dorsal sides upward, clinging close to each other. The sarcopterygians are considerably flattened. The orientation of the specimens is various, it tend to be submeridional for asterolepids, sublatitudinal for the lobe-finned fishes (Lyarskaya 1981, p.39; fig. 11). It seems that such orientation must have been determined by the different size and weight of the body in these distinct groups (Upeniece, 2001b): weak bottom currents rather easily transported the cadavers of asterolepids contrary to the big and heavy sarcopterygians, which possibly were trundled over the bottom of the basin until buried and resulted in a sublatitudinal orientation. In early Frasnian the clastic supply directions in the East Baltic were mostly from north to south (Fig. 1.1).

### 3.3. Types of fossil fish taphocoenoses

The Devonian vertebrate localities of Latvia had been classified into four types by Lyarskaya (1972a). Five types of taphocoenoses are divided and analysed in correlation with lithological type of siliciclastic deposits of the Lode Formation in the Lode pit (Upeniece, 1991, 1999; Kuršs et al., 1998, 1999). The sixth and the seventh types of taphocoenoses in the Lode quarry correspond to the medium and coarse-grained sandstones of the Gauja Regional Stage (Tables 3.2., 3.3.).

Taphocoenosis of the **first type** (Figs. 1.3., 3.1.) had been formed a weak currents and is characterized by the high degree of preservation of organism remains. Organism remains were accumulated in the clayey mud which filled local depressions in the sandstone on the submarine delta slope. The organism assemblage includes small sized remains: more or less complete skeletons of fish juveniles (about 1-4 cm in total length) of placoderms *Asterolepis ornata*, acanthodians *Lodeacanthus gaujicus*, sarcopterygians *Strunius* sp. nov., Osteolepididae gen. et sp. ind., *Latvius* sp. nov., actinopterygians *Cheirolepis* sp., coelacanths, as well as mysidacean, conchostacan, ostracod crustaceans, eurypterids, and plant micro- and macroremains. Fine dispersed clay is characterized by microbedding horizontal texture, as well as by frequent red interlayers of the fine dispersed clay. All organism remains are black or dark brown in colour.

Some very leached, black skeletons of complete adult individuals of placoderm *Asterolepis ornata* were found in the above mentioned clay lens. Near to the eastern slope of the depression a complete large skeleton of *Laccognathus panderi* occurred in excavations in 1998 by the author. The total length of individual comprises over than 1.65 m, exceeding complete individuals known so far (Kuršs *et al*. 1999).

Taphocoenosis of the **second type** is distinguished in the fine-dispersed clay and silty clay. In excavations of 1971, 1972, 1976, carried out by L. Lyarskaya, about a hundred complete adult individuals of placoderm *Asterolepis ornata* were found in several fish-bearing layers, mentioned in the chapters 1.2 and 3.2. Several carcasses of sarcopterygian *Laccognathus panderi* and two skeletons of *Panderichthys rhombolepis* also occurred. The orientation of skeletons is submeridional (Layrskaya, 1972, Fig. 2). The complete skeleton of sarcopterygian *Eusthenopteron kurshi*, excavated by I. Zupiņš at the end of 1990-ies (Zupiņš, 2008), as well as a few other finds and well-preserved crustaceans and plant remains correspond to this type of taphocoenosis. This type of taphocoenoses does not contain juvenile individuals of fish and have been formed in a slightly higher water activity to compare with the previous type of taphocoenoses.

Table 3.2. Types of the taphocoenoses correlated to the lithology of the Gauja Regional Stage and paleoenvironment of burial in the deltaic regions

3.2. tabula. Tafocenožu tipi saistībā ar iežu tipiem Gaujas reģionālajā stāvā un paleovide deltu reģionā

| **Lithological types** | **Bedding** | Hydrodynamic regime | Type of taphocoenosis | **Organism remains** |
|---|---|---|---|---|
| Fine-dispersed dark grey clay (laminites) | micro-planar, parallel lamination | very weak currents, fallout without traction | 1 | Well preserved whole skeletons of fish juveniles (placoderms, acanthodians, sarcopterygians etc.), a lot of crustaceans, plant fragments and coprolites. |
| Fine-dispersed greyish-yellow clay | weak planar or massive | very weak current or stagnant water | 2 | Well preserved whole skeletons of adult fish (placoderms and sarcopterygians), plant fragments. |
| Fine-dispersed greyish-yellow clay | weak planar or massive | very weak current | 3 | Well preserved articulated skeletons of adult fish (placoderms and sarcopterygians) with weakly disarticulated scale covering, rarely disarticulated bones and scales. |
| Red siltstone and silty clay | massive | gentle current | 4 | Articulated and disarticulated plates, bones, scales of placoderm and sarcopterygian fish. |
| Fine-grained greyish-blue sandstone | cross-stratified and ripple-laminated | moderately rapid current | 5 | --“-- |
| Medium and coarse-grained sandstone | --“-- | rapid current | 6 | Rarely complete bones, often fragments of fish bones |
| Conglomerates |  | --“-- | 7 | Rounded fragments |

Taphocoenosis of the **third type** (Fig. 3.7.) consists of disintegrated to various degrees skeletons of *Asterolepis ornata,* described in detail in the previous chapter. Such fossils have been observed within this type of taphocoenosis: 1) articulated skeletons without jaw and orbital bones, 2) skeletons without or pushed out AMD plate, 3) skeletons with disintegrated or without caudal parts, as well as 4) separate body parts. Small vertical burrows directly under the fish-bearing layer indicate activity of organisms tolerant to low oxygen level. The fast termination of the small vertical burrows would point to the rapid sedimentation of clayey mud and cessation of the oxygen.

The fish remains from the described above three taphocoenoses seemingly had not undergone the floating stage, and transportation to burial place was not durable. Disintegration process continued in the clayey mud of burial place.

Taphocoenosis of the **fourth type** occurs in the red/greyish-blue siltstone with indistinct planar bedding as deposited in a regime of low water activity. The remains occur in spotts and abundantly: a number of bedding planes of well-preserved plates, fins and body parts of *Asterolepis ornata,* lot of scales, teeth, as well as separate head and bones of shoulder girdle of *Laccognathus panderi* were excavated and drawn by the author in 1991 (Fig. 3.9.). In one case some skeletons of *Asterolepis ornata* (without caudal parts) have been excavated. Remains always are white or light grey.

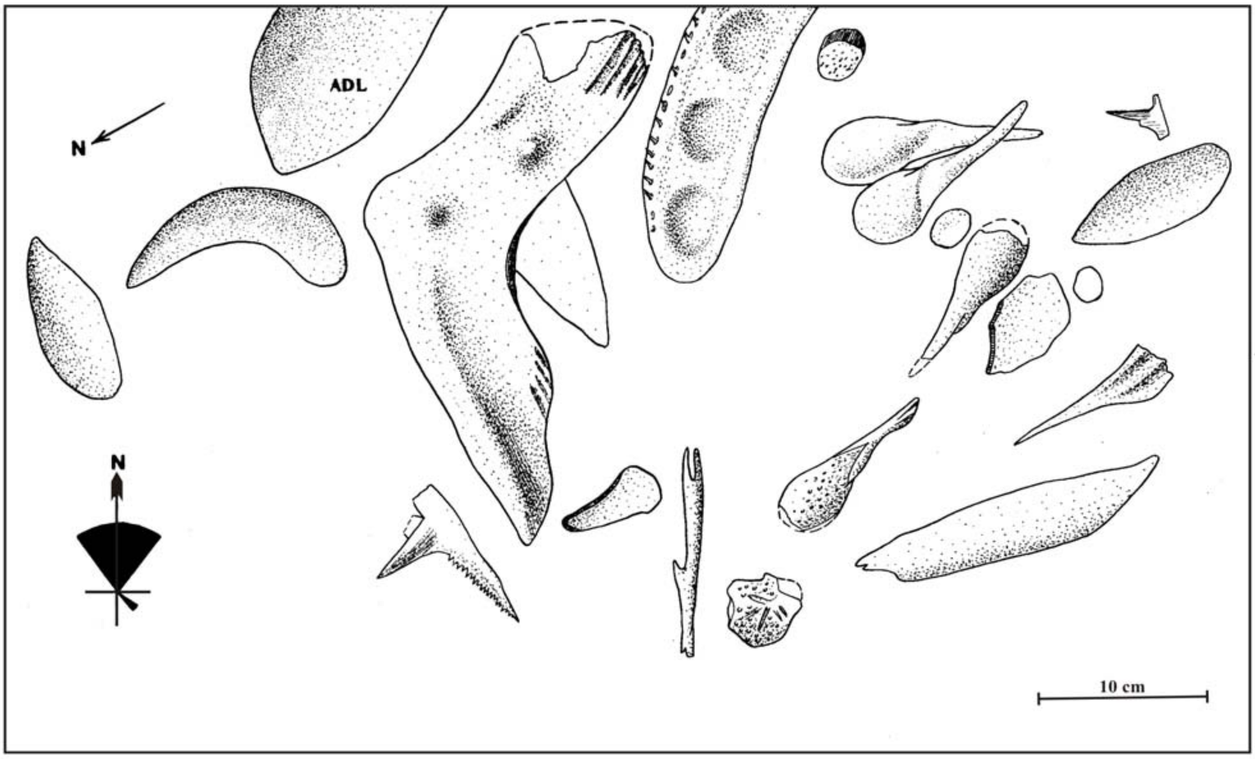


Fig. 3.9. Distribution of fish remains in the taphocoenosis of the fourth type (Kuršs *et al*. 1999, Fig. 1). The remains of sarcopterygian *Laccognathus panderi* dominate this taphocoenosis. ADL, the fragment of the anterior dorsal lateral plate of placoderm *Asterolepis ornata*.

3.9. att. Zivju atlieku izplatība 4.tafocenožu tipā (Kuršs *et al*. 1999, Fig. 1). Tafocenozē dominē daivspurzivju *Laccognathus panderi* atliekas. ADL, bruņuzivs *Asterolepis ornata* priekšējā muguras-sānu bruņu plātne.

These siltstones are often interbedded by cross-stratified and ripple-laminated fine-grained greyish-blue sandstone. Measurements of cross-beds show southeasterly direction of paleocurrents, which corresponds to general orientation of streams during the Gauja time. Sediments were deposited by currents of moderate velocity in a shallow-water environment forming taphocoenosis of the **fifth type**, containing abundant remains of well-preserved disarticulated plates, bones, scales and teeth of the above mentioned fish genera. The high degree of the disintegration indicates either the durable transportation or the disintegration of skeletons in insufficient quantity of covering sediments.

Fish remains within the taphocoenosis of the fourth and fifth type have undergone the disintegration process before final burial, including transportation and possibly floating stage. The abundance of fossil remains could be explained by changing velocity of currents or irregular bottom of basin.

Taphocoenosis of the **sixth type** in the Lode quarry corresponds to the medium- and coarse-grained sandstones of the Gauja Formation containing fish-bearing lenses and layers consisting of unbroken scales, teeth, as well as fragments of fish bones (*Asterolepis ornata, Laccognathus panderi, Psammolepis* sp.), and fulcral scales of psammosteids. These remains had undergone more durable transportation process. In one case the whole branchial plate of *Psammolepis paradoxa* occured.

The above mentioned medium and coarse-grained sand was accumulated by rapid currents in the wave zone of marine deltaic environment (Kuršs, 1975). These sediments are often forming slump depressions filled with brecciated material. The organism remains are fawn-coloured; sediments are reddish, coloured with iron compounds from the crust of weathering (Kuršs, 1975). Dispersed clay in the central parts of these depressions forms the first and second types of taphocoenoses.

It must be noted that the sandstone containing conglomerates of fish remains, are often visible mostly in the basal parts of the Gauja Regional Stage (outside the Lode pit). These taphocoenoses correspond to the separate type of taphocoenosis of the **seventh type**.

Table 3.3. A comparison of organism assemblages of the Lode and Gauja Formations
(Kuršs *et al.*,1999, Table 1, with modifications)
3.3. tabula. Lodes un Gaujas svītu organismu taksonu salīdzinājums
(Kuršs *et al.*,1999, Table 1, ar izmaiņām)

| Taxa | Types of the taphocoenoses in the Lode quarry | | | | | | Gauja Fm. * |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| **Vertebrata** | | | | | | | |
| *Psammolepis paradoxa* Agassiz | | | | + | | + | + |
| *Psammolepis alata* Mark-Kurik | | | + | | | | + |
| *Psammolepis undulata* (Agassiz) | | | | | | | + |
| *Psammolepis heteraster* Gross | | | | | | | + |
| *Psammosteus* sp. | | | | | | + | + |
| *Plourdosteus livonicus* (Eastm.) | | | | | | | + |
| *Asterolepis ornata* Eichwald | + | + | + | + | + | + | + |
| *Asterolepis ornata* Eichw. (juveniles) | + | + | | | | | |
| *Devononchus concinnus* (Gross) | | | | | | | + |
| *Devononchus laevis* (Gross) | | | | | | | + |
| *Haplacanthus ehrmanensis* Gross | | | | | | | + |
| *Homacanthus gracilis* (Eichwald) | | | | | | | + |
| *Nostolepis gaujensis* Valiukevičius | | | | | | | + |
| *Lodeacanthus gaujicus* Upeniece | + | | | | | | |
| *Miguashaia grossi* Forey, Ahlberg, Lukševičs, Zupiņš | | + | | | | | + |
| *Glyptolepis baltica* Gross | | + | | | | | + |
| *Laccognathus panderi* Gross | + | + | + | + | + | + | + |
| *Grossipterus crassus* Gross | | | | | | | + |
| Dipteridae | | + | | | | | |
| *Strunius* sp.nov. | + | | | | | | |
| *Latvius* sp.nov. | + | | | | | | |
| *Eusthenopteron kurshi* Zupiņš | | + | | | | | |
| Osteolepididae | + | | | | | | |
| *Panderichthys rhombolepis* (Gross) | | + | | | | | + |
| *Cheirolepis* sp. | + | | | | | | |
| **Invertebrata** | | | | | | | |
| Mysidaceae | + | + | | | | | |
| Conchostraca | + | + | | | | | |
| Ostracoda | + | | | | | | |
| Merostomata | + | | | | | | |
| Parasitic worms Platyhelminthes | + | | | | | | |
| Brachiopods Cyrtospiriferidae | | | | | | | + |
| “Camarotoechiidae” | | | | | | | + |
| *Bicarinatina* aff.*parva* (Batrukova) | | | | | | | + |
| Stromatoporata (several forms) | | | | | | | + |

|  | 1 | 2 | 3 | 4 | 5 | 6 |  |
|---|---|---|---|---|---|---|---|
| **Flora** |  |  |  |  |  |  |  |
| *Svalbardia polymorpha* Hoeg | + |  |  |  |  |  |  |
| *Archaeopteris fissilis* Schmal. | + |  |  |  |  |  |  |
| *Archaeopteris* sp. |  | + |  |  |  |  |  |
| *Rhacophyton* sp. |  | + |  |  |  |  |  |
| *Platyphyllum* sp. | + |  |  |  |  |  |  |
| *Trochiliscus* (?) sp. | + |  |  |  |  |  |  |
| *Nematophyton* sp. |  | + |  |  |  |  | + |

* After: Sorokins et al., 1981; Lyarskaya, Lukševičs, 1992; Valiukevičius, 1998.

### 3.4. Trophic relations within the Lode faunal and floral assemblage

Previously studies on trophic relations of the Devonian organisms were done by several authors: Mark-Kurik (1995) for the Eifelian, and Lebedev (1992) and Lukševičs (1992) for the Famenian. Lode faunal and floral assemblage reflects more various food chains due to excellent preservation of variety of organisms. The trophic pyramid typical for the Devonian palaeobiocenosis of the delta area is created for the first time (Fig. 3.6).

The Devonian seas in the Baltic region were located on the continental shelf, thus being epicontinental, comparatively shallow and favourable for development of rich fauna and flora (Kuršs, 1992b). Deltaic area was extremely favourable for coexisting of representatives of different major taxa. The high density of fish populations in deltaic regions was determined by the abundance of their presumed food resources including small invertebrates and plant detritus. Marvellous preservation of the specimens indicates that they were brought in from nearby environments.

The Lode assemblage is characterised by rather high biodiversity of Devonian vertebrates and invertebrates (Table 1.1). Most Devonian taxa of vertebrates are present: heterostracan agnathans, placoderms, acanthodians, sarcopterygians, and actinopterygians. The list of vertebrates from Lode includes 15 fish species; four of them are typical only for the Lode Formation (Table 3.3). Both adult and juvenile individuals are presented by several species. The local abundance of mysidaceans and conchostracans makes an ideal link in the food chain between algal phytoplankton and carnivorous fish in the trophic levels of the Lode organism assemblage (Upeniece, 2001b). Dominance of placoderm *Asterolepis ornata* may reflect an expansion of the species in the absence of large predators, carnivorous arthrodires, which are characteristic for the Gauja Regional Stage.

The limited occurrence of young fish in only one clay lens at the Lode quarry suggests that they may have lived in restricted areas, suitable for spawning (near mouth of a big river). Fishes of similar size grouped together during their life cycle. The juvenile fish-assemblage combines forms from different habitats: including predaceous forms, plankton feeders and benthic forms. The ratio between them (asterolepids, acanthodians and sarcopterygians) comprises about 50:7:1 (Upeniece, 2001b). Agnathans are totally absent in this bed. The small fish probably were seeking the protection of the shallows and aquatic vegetation.

Trophic hierarchy of the Lode organism assemblage is proposed (Fig. 3.10.) presuming the autochthonous character of burial. Almost complete absence of coarse-grained material in the Lode clays and perfect state of preservation of fish and invertebrates, as well as the remains of well-preserved inflowed terrestrial plants *Archaeopteris fissilis* and *Svalbardia polymorpha* suggest, that this assemblage (taphocoenoses type 1) may reflect palaeobiological community (Upeniece, 2000). Although the very seldom finds of several detached bones of an actinistian *Miguashaia grossi* could indicate its different living area. Nevertheless, it could have to occupy the level of the larger predators.

Feeding relations are based on the structure of the mouth and jaw apparatuses, body form and size. All feeding modes of fish are represented: benthos- and zooplankton feeders, detritivores, herbivores and carnivores. Vertebrates were capable of feeding in different ways as the majority of the extant fishes do, that is, several species in the trophic level reconstruction represent both the primary and the secondary consumers (e.g. phyto- and zooplankton feeders).

The Lode organism assemblage is featured by variety of predatory fishes (9 species). Characteristic is the almost complete absence of juveniles of the greatest predators. The most abundant prey fishes in Lode are *Asterolepis ornata*, *Psammolepis alata, Lodeacanthus gaujicus*, as well as juveniles of sarcopterygians *Strunius* sp. nov., *Latvius* sp. nov. and actinopterygian *Cheirolepis* sp.

The high level hierarchy is characterized for the Lode assemblage. Food chain (arrows, Fig. 3.10.) shows the transfer of energy from the producers (algae and green plants) through a series of organisms that eat and are eaten. A series of interconnecting food chains represents the feeding relationships of organisms within a palaeoecosystem. Trophic level represents a step in the transfer of food or energy within a chain. Several evidences of food chains found in the fossil material are described below.

There are several trophic levels within the Lode palaeoecosystem: producers, primary consumers, secondary consumers; the predators form fourth and fifth levels (Fig. 3.10.). The base of the trophic hierarchy is composed of producers - autotrophic organisms (algae and phytoplankton) and organic detritus. The primary consumers include benthic forms (detritivores and herbivores), zooplankton and small nekton (acanthodians); the secondary consumers are benthos- and zooplankton feeders. Two levels of predators represent the tertiary consumers: small predators and top predators (large ones). The fish parasites must have formed the final sublevel of predators, although they are found still only in the bodies of primary consumers (juveniles of *Asterolepis ornata* and *Lodeacanthus gaujicus*, as well as in small crustaceans).

### *PRODUCERS*

Trophic relations in each ecosystem start with the level of producers. In the Lode organism assemblage they are represented by:

**1. Algae** are represented by well preserved remains of *Platyphyllum* sp. The megaspores and oogonia of charophyte algae are observed also.

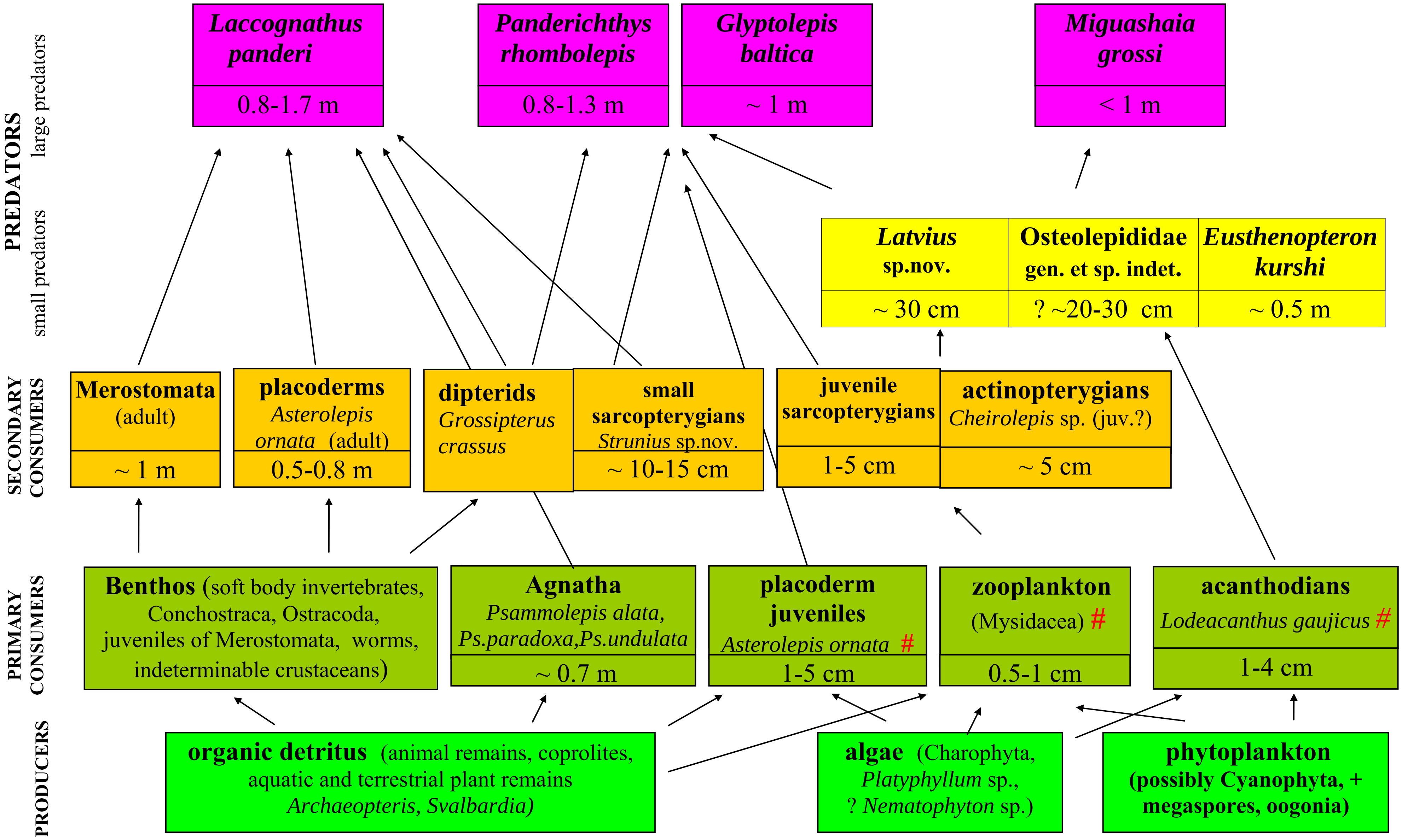
**2. Phytoplankton** remains of undetermined taxa.

**3. Organic detritus** of various origin:

1) well-preserved fragments of terrestrial plants *Archaeopteris fissilis, Svalbardia polymorpha*, and aquatic plants *Platyphyllum* sp. are abundant;

2) thousand of coprolites of various forms, size and inclusions imply that they belonged to the wide range of fishes;

Fig. 3.10. Proposed trophic relations of the Lode organism assemblage (# - infested by parasites)
3.10. att. Iespējamās barības ķēdes Lodes organismu paleobiocenozē (#- ar parazītu atliekām)



3) plenty remains of soft body organisms or their parts are inductively traced in the clay ‘’bubble’’ structures, which must have originated due to decomposing gases, limited from around by decaying soft parts (Upeniece, 2000, 2001b);
4) remains of dead organisms.

Autotroph organisms together with the microremains of plant material and organic detritus form the base of food for primary consumers.

### *PRIMARY CONSUMERS*

#### ***Invertebrates***

**1. Benthic organisms.** Detrite feeders are represented by: 1) rare Ostracoda, which could have fed on remains of terrestrial plants as do the recent forms; 2) abundant Conchostraca, fed on phyto- and zooplankton; 3) juveniles of Merostomata represented by some finds of disarticulated remains; 4) soft bodied invertebrates, and 5) possible worms, evidenced by ichnofossils.

**2. Zooplankton** is represented by abundant Eumalacostraca (Mysidacea). Thousands of these small mysidacean crustaceans (with the length 0.5-1 cm formed several bedding planes and could have supported the level of secondary consumers. Mysidaceans have been fed on microzooplankton, and possibly on algae. The finds of the content of mysidacean intestine with carbonized remains implied to that. About 90% of mysidaceans had been found in the upside-down position, implying on the post-mortem accumulation.

#### ***Vertebrates***

**3. Detritivore** organisms are represented by juveniles of placoderm *Asterolepis ornata.* The length of them ranges from about 1 to 5 cm. Full stomach content in a great number of juveniles gives a clue to their mud-grubber habitats. Stomach contains small fragments of bones and scales, as well as carbonized plant detritic material and quartz grains. In detail it will be dealt in the 4.1. chapter devoted to the morphology of juveniles of *Asterolepis ornata.*

**4. Detritivore and benthophagous** organisms are represented by heterostracans *Psammolepis alata, Ps. paradoxa* (primary and secondary consumers). Psammosteid heterostracans, possessing somewhat dorsally placed toothless mouth and specific tail ensuring slanted position of the body during feeding (as seen in the reconstruction by Obruchev, 1944), were most probably organic detritus, benthos and plankton feeders. The average length of them comprises about 0.7 m. These agnathans could possibly also consume small arthropods, fish fry etc. (Mark-Kurik, 1995).

### *SECONDARY CONSUMERS*

**1. Benthophagous** organisms are represented by plenty adult individuals of placoderm *Asterolepis ornata,* reflecting the most abundant fish. The average length of them comprises about 0.5-0.8 m. The ventral mouth, weak jaws and absence of tooth indicate herbivory. The food specialization changed during the lifetime of asterolepids. The juveniles fed on organic detritus as it is seen from their well-preserved stomach content. Adults could have fed on the soft-bodied and small shelly invertebrates also (Ostracoda, Conchostraca). On the supposedly detritophagous mode of life of the latter was marked earlier also (Karatajūte, 1958b; Denison, 1978).

**2. Planktivorous** organisms are represented by acanthodians *Lodeacanthus gaujicus.* Their occurrence is rather frequent and they represent the primary and secondary consumers. Streamlined fusiform acanthodian *Lodeacanthus* were toothless planktonivorous forms of the 3rd trophic level. Absence of teeth indicates a non-predatory lifestyle and probably these fishes were browsers which might have fed on weeds or algae.

These small fishes (1-4 cm) must have swam in schools and support the sublevels of tertiary and quartenary consumers (carnivores). (The finds of *Haplacanthus* sp. in neighbouring fossil site "Cēsu glūda" of the same Lode Formation could have give complementority to the palaeoecology of the area.)

**3. Juveniles of sarcopterygians** also could have been included in the level of secondary consumers. There are only few finds of juvenile individuals *Strunius* sp.nov. and *Latvius* sp.nov. The length of them comprises about 1-5 cm.

**4. Small sized fishes** are known by finds of adult of *Strunius* sp.nov. with the length about 10-15 cm, as well as of very few fragments (5 cm long) of actinopterygian *Cheirolepis* sp. and dipterids *Grossipterus crassus*.

**5. Merostomata** are known by finds of fragments of the segments of adult individuals, supposedly eurypterids. The average length of animals could reach about 1 m.

### *TERTIARY CONSUMERS (PREDATORS)*

**1. Largest predators.** The top consumers are supposed to be the largest predators *Laccognathus panderi, Panderichthys rhombolepis* and *Glyptolepis baltica,* as well as probably an actinistian *Miguashaia grossi.* The average length of them comprises about 1 m. They must have been fed on the smaller predators and secondary consumers, mentioned above. Predator-ambuscader *Panderichthys rhombolepis,* which had a flat skull with dorsal eyes possibly could have a something crocodilian-like mode of life. Their finds are restricted only to the seldom finds of complete skeletons.

**2. Smaller predators.** A lower trophic level was occupied by smaller predators: *Eusthenopteron kurshi*, *Latvius* sp., *Strunius* sp., and medium-sized undetermined osteolepid fish. The average length of them comprises about 20-50 cm. This level supposedly includes also subadult stages of the larger predators, mentioned above. The food specialization of smaller predators was probably restricted to the abundance of smaller fishes (1-4 cm): both juveniles and adults of acanthodians *Lodeacanthus gaujicus* and juveniles of placoderm *A. ornata.*

### *FISH PARASITES*

Fish parasites form the highest level of the trophic hierarchy in the Lode assemblage. High degree of fish invasion is similar to what may be observed in the extant forms. For example, 43 young fish bodies of *Asterolepis ornata* and *Lodeacanthus gaujicus* were find infested by 77 individuals of parasitic helminths. Two individuals of parasites were found in crustacean Mysidacea indet., and two beside the conchostracans. These form the oldest parasitic association ever found in the fossil record (Upeniece, 1998; 1999 a,b,c; 2000, 2001; Poinar, 2003). In detail it is described in the 3.1.chapter devoted to the distribution of fossils in the "juvenile fish" lens.

# 4. Morphology and ontogeny of juveniles of placoderm *Asterolepis ornata* Eichwald sensu Agassiz

Placoderms are extinct jawed fishes which almost entire evolutionary history was confined within a single geological period, the Devonian. Placoderms have elongate box-like body armour that completely encloses the pectoral fin base in dermal bone. The dermal armour is made up of two parts; it covers the head and the anterior part of the trunk. In most of these fishes there is a bony joint between the head and trunk armour, unlike anything seen in other jawed fishes or the ostracoderms. The placoderms are often well preserved due to their dermal armour, but articulated specimens are rarely found.

The antiarchs, to whom the finds of *Asterolepis* juveniles belong, are an early superorder of armoured jawed fishes Placodermi. The Antiarchi is considered to be one of the highly specialised forms among the vertebrates in regards of their shoulder girdle and pectoral fin. Their wide geographical distribution has made them a key group in attempting to understand Devonian biogeography (Young, 1984a, 1993) and particularly for testing Middle and Late Devonian continental reconstructions (Young, 1990a). The antiarchs have been much used in biostratigraphical zonations of the Middle and Upper Devonian sediments on and peripheral to the Old Red Sandstone continent (Karatajūte, 1958a; Young, 1974; Blieck *et al.*, 1988). The antiarch zonation is best developed in the East Baltic, where species lineages within single genera are established (Lyarskaya, 1981; Esin *et al.*, 2000).

The genus *Asterolepis* has been intensively studied for correlating and assessing the age of rock sequences in the East European platform (Gross, 1942; Karatajūte, 1958a; Karatajūte-Talimaa, 1963) and in East Greenland (Marshall, Astin, 1996). *Asterolepis* is used in the vertebrate zonation and correlation of the Givetian and Frasnian sediments of the Baltic area and Scotland (*A. orcadensis, A. thule, A. maxima*), north-western Russia (*A. dellei, A. ornata, A. radiata*), and North Timan (*A. radiata*).

*Asterolepis* has been recorded with full certainty from the Baltic States, Russia (north-western Russia and Timan), Scotland, Spitsbergen, East Greenland and USA, e.g. the area of its distribution coincides with the Euroamerican paleocontinent. This genus is represented by 13 named species and 11 unnamed species, from that 7 and 4, respectively, are restricted mainly to the Main Devonian Field (East Baltic area: Estonia, Latvia, Lithuania, north-western part of Russia and Belarus). The first appearance of the genus *Asterolepis* is known from the Emsian of Belarus (Mark-Kurik, 2000, p.320). The genus reaches its widest distribution in the late Givetian and early Frasnian: a number of species are recognized in the Main Devonian Field, Scotland, East Greenland, France, Belgium, Spitsbergen (summarized in: Upeniece, 2002).

Several authors have been studied morphology of adult *Asterolepis ornata*. Pander made the first reconstruction of *Asterolepis ornata* (1857); it was based on the disarticulated, mainly fragmentary material from the outcrops along the river Gauja. Eichwald gave the diagnosis of the genus and some species (1860), although Agassiz was the first who correctly used the name *Asterolepis ornata* for the fossils from the Gauja Regional Stage (1845). Gross described and excellently figured the majority of the armour plates, presented a new reconstruction of the head and trunk shields from the dorsal and lateral views, histological description of different bone plates, as well as the patterns of head's and pectoral fin's movements (1931, 1933a). Karatajūte-Talimaa described asterolepidoid morphology, habitats and gave a whole-bodied reconstruction (1957, 1958b, 1963). Lyarskaya described morphology and provided the first reconstruction, based on the findings of the whole-bodied skeletons (1972b, 1977, 1981), including caudal part, orbital fenestra and the mouth apparatus. A new reconstruction of the caudal part followed in 1996 (Ivanov, Lukševičs, Upeniece), and of the orbito-nasal cavity as well (Lukševičs, 2001b).

The maximal length of the dermal armour of adult individuals of *Asterolepis ornata* is about 38 cm; the total length of the fish body comprises around 60-65 cm (Lyarskaya, 1981, p. 96). Bit longer length of the ventral wall of the same species, reaching about 40 cm, is mentioned in Nilsson (1941, p. 27; after the W.Gross letter).

## 4. 1. Morphology of juveniles of *Asterolepis ornata*

### 4.1.1. General remarks

Unique material of complete juvenile armoured fish (Vertebrata, Placodermi, Antiarchi) is presented from the Upper Devonian, Lode Formation of Latvia, Lode clay quarry. It comprises the sequence of the previously unknown earliest growth stages of placoderm juveniles and belongs to an antiarch fish genus *Asterolepis*. This represents the first record of juveniles of the genus *Asterolepis* (Upeniece, Upenieks, 1992). These are the smallest and the best preserved antiarch juveniles ever recorded so far in the fossil record in the world (Fig. 4.1.).

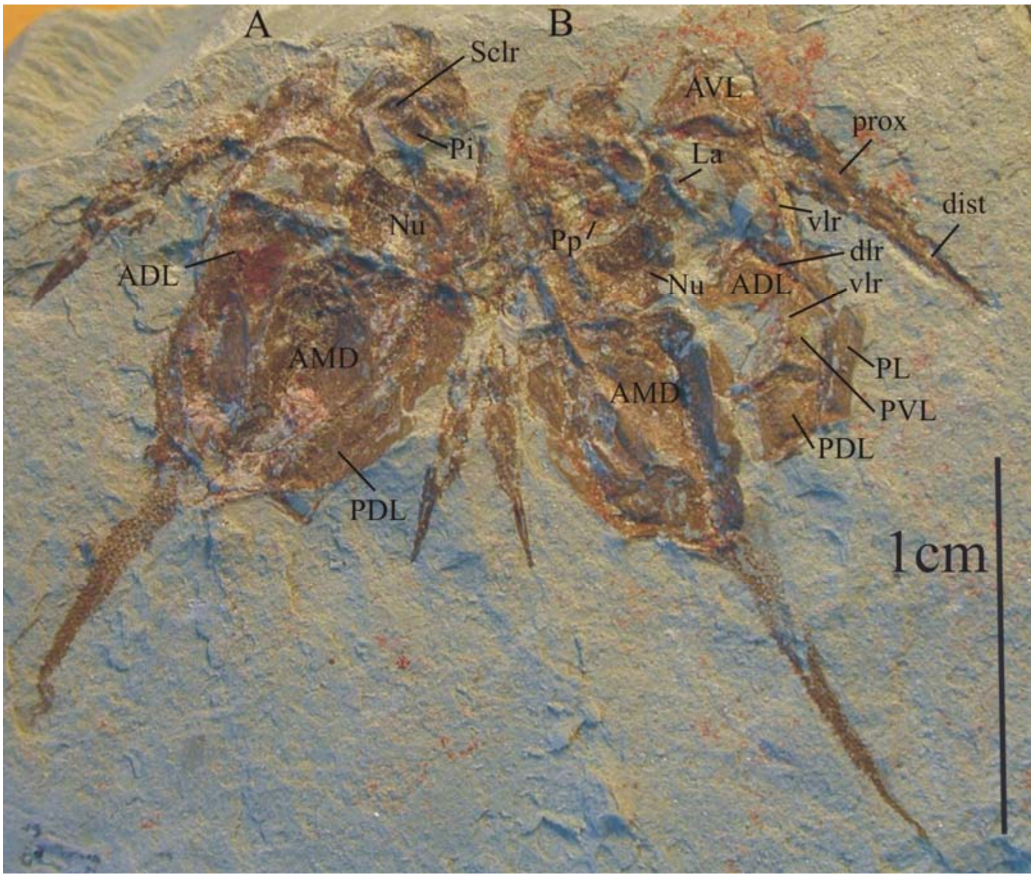


Fig. 4.1. Two completely preserved juveniles of *Asterolepis ornata*. Mainly the visceral view of the dorsal wall exposed. Upper Devonian, Lode Formation, Liepa (Lode) clay pit, Latvia. **A**, LDM 260/223. **B**, LDM 260/224.

4.1. att. Divi pilnīgi veseli saglabājušies bruņuzivju *Asterolepis ornata* mazuļu skeleti. Dorsālo sienu iekšskats. Augšdevons, Lodes svīta, Liepas (Lodes) mālu karjers, Latvija. **A**, LDM 260/223. **B**, LDM 260/224.

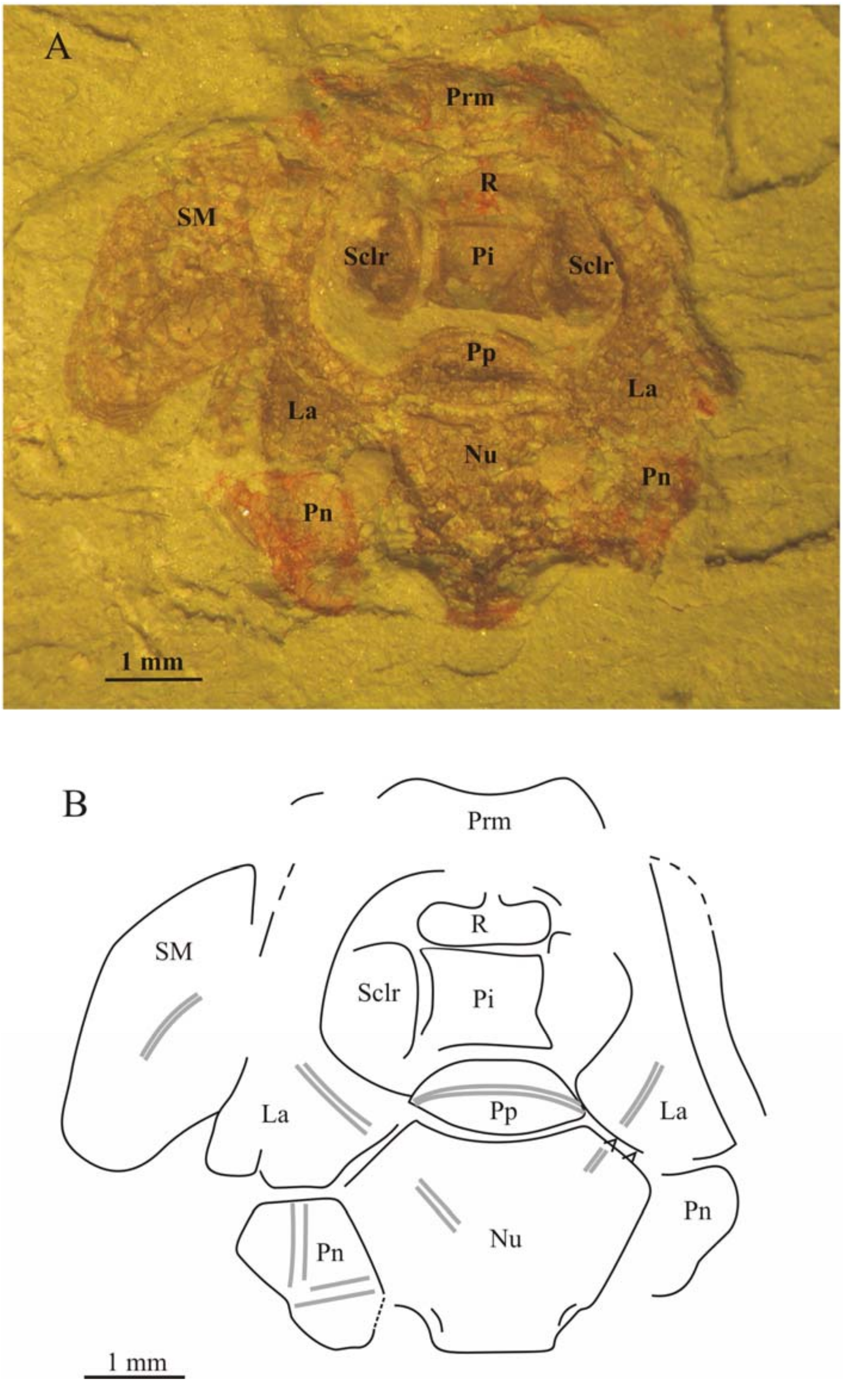


Fig. 4.2. Head shield of juvenile of *Asterolepis ornata* from the Liepa (Lode) pit: **A,** LDM 260/266a, in visceral view. **B,** LDM 260/266a,b, drawn on part and a counterpart.

4.2. att. Bruņuzivs *Asterolepis ornata* mazuļa galvas vairogs. Liepas (Lodes) karjers. **A,** LDM 260/266a, iekšskats. **B,** LDM 260/266a,b, kombinēts zīmējums no abām parauga pusēm.

According to morphological features the juveniles under consideration belong precisely to the genus *Asterolepis* (Figs. 4.2.; 4.3.; 4.4.): 1) the nuchal plate is excluded from the posterior border of the orbital fenestra by the postpineal plate; 2) the AMD plate is in contact with the MxL (in juveniles MxL consists from the PDL plus PL plate) plate along its posterolateral edge; 3) the semilunar plates are paired; 4) the pectoral fins consist of the distal and the proximal segments. Index of anatomical abbreviations used for placoderms is given in the appendix No 1.

All material of *Asterolepis* juveniles is referred to the species *Asterolepis ornata* Eichwald sensu Agassiz because of large occurrence of adults of the representatives of mentioned single genus and species in the Lode quarry and Lode Formation at all. The Lode Formation comprises the upper part of the Gauja Regional Stage. The second species occurring in the Gauja Regional Stage is *Asterolepis essica.* It is known from the single locality near the village Essi, Estonia (lower part of the Gauja Regional Stage), and is represented by a head-shield and few disarticulated trunk plates (Lyarskaya, 1981). Therefore a large number of mentioned above finds of juvenile of *Asterolepis* obviously should be referred to the species *Asterolepis ornata.*

The juveniles of *Asterolepis ornata* are excellently preserved, providing morphological details, unknown for the adults. Changes of morphological features of young individuals during the ontogenetic development are described and figured below. Juveniles reveal reticular ornamentation, which in larger juvenile individuals gradually changes into radial ridges and then into tubercules characteristic already for the adult individuals.

Due to the thin dermal armour the juveniles are much dorso-ventrally flattened. Only little part of the specimens were preserved compressed laterally allowing the investigation of the lateral walls. All skeletal remains are dark-brown or black in colour.

### 4.1.2. Size and general proportions

**Size.** There is a rather limited size range in the material - all specimens are of small size. Nevertheless the sequence of the earliest growth stages of the dermal armour and squamous part is presented. A total length of the dermal armour (head and trunk shields) of the smallest articulated juvenile individual (Fig. 4.43. B) comprises 10.4 mm. The estimated total length of the dermal armour of the largest juvenile represented in the material is about 38.0 mm. Young individuals of *Asterolepis ornata* morphologically resemble adult ones when the length of the dermal armour reaches about 4 cm (Fig. 4.47.). The measurements, indicated dimensions of the head-shield and trunk armour plates, as well as overall proportions of the armour plates during the growth are given in the appendix No 2.

Several articulated juvenile individuals with wholly preserved squamous part exhibit total length of the entire body (total dermal armour plus tail): it ranges from 20.2 to 33.2 mm (Ivanov *et al*., 1996, Table 1).

The minimum size of *Asterolepis ornata*, i.e. the size at hatching, is not clear. The smallest measurable specimen (Fig. 4.43. B) has a length of trunk shield of 6.4 mm and estimated length of the head shield of 4.0 mm; therefore the estimated total armour length could be 10.4 mm, as mentioned above. There is, however, a little smaller but disarticulated specimen (Fig. 4.43. A), from which the complete and measurable length of AVL plate comprises 5.5 mm (in the former specimen, respectively, 6.1 mm). The dermal armour of

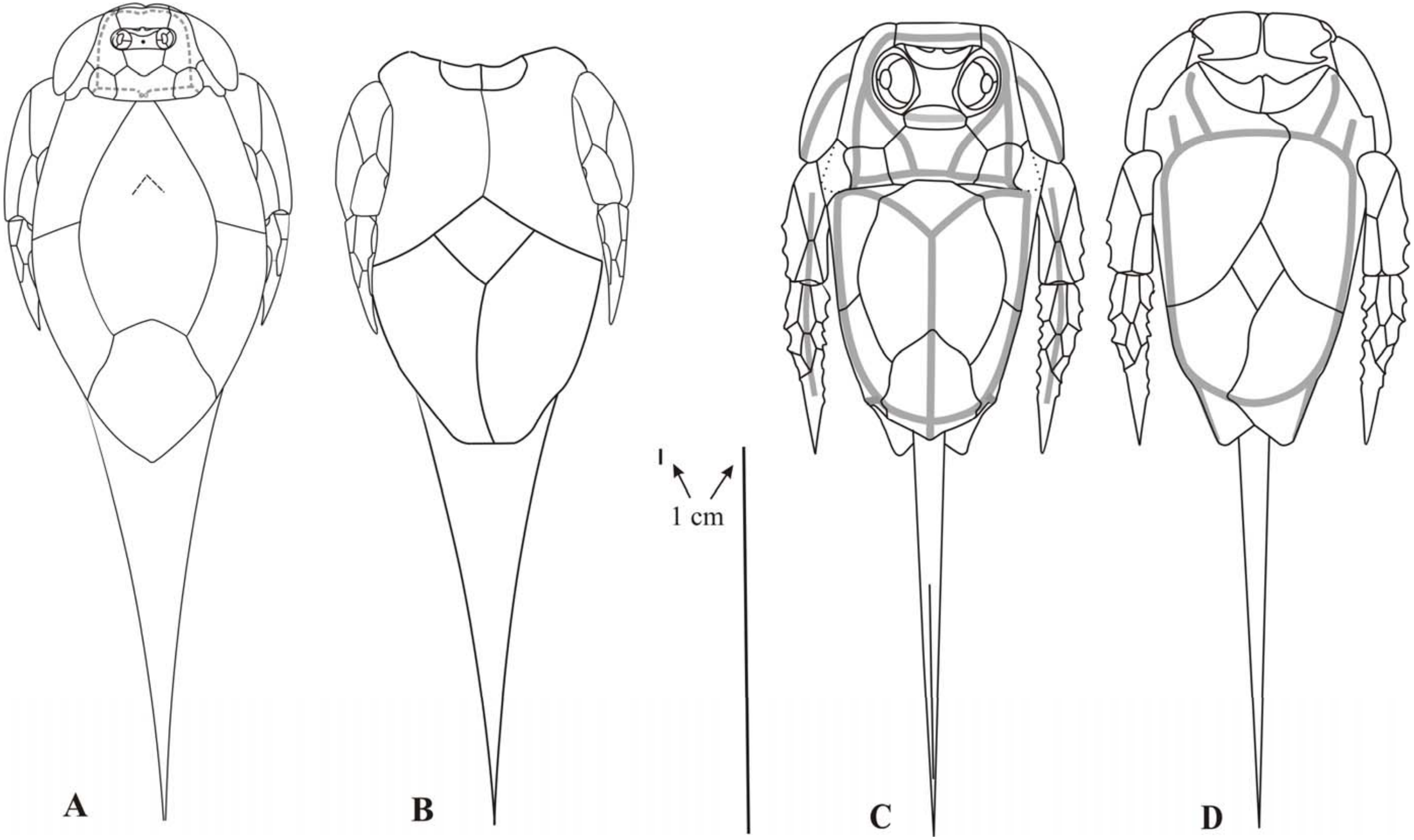


Fig. 4.3. **A, B**, Reconstruction of adult *Asterolepis ornata* (Lyarskaya, 1981, Fig. 74, with slight modifications in semilunar area). A, dorsal side. B, ventral side. **C, D**, Reconstruction of juvenile *Asterolepis ornata* (Upeniece, Upenieks, 1992, Figs. 2B, 3B). Grey solid lines indicate ridge system. C, dorsal side. D, ventral side.

4.3. att. **A, B**, Pieaugušas bruņuzivs *Asterolepis ornata* rekonstrukcija (Lyarskaya, 1981, Fig. 74, ar nelielām izmaiņām semilunāres reģionā). A, mugurpuse. B, vēderpuse. **C, D**, Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija (Upeniece, Upenieks, 1992, Figs. 2B, 3B). Pelēkās līnijas iezīmē valnīšu sistēmu. C, mugurpuse. D, vēderpuse.

these specimens is very thin and translucent. Obviously, the smaller individuals had not developed their dermal armour to such an extent that it increased fossilization potential significantly. Due to the very thin dermal armour the plates are partly flexible, as they appear to be crinkled and folded over one another. Reticular ornamentation occurs on the plates' ossification centres, leaving the rest of the area smooth.

The predominant part (over 90%) of the specimens is similar-sized individuals with the total dermal armour length of 14.0-16.0 mm. These over than 300 specimens could have been individuals from the one spawn (Figs. 4.1.; 4.2.; 4.5.).

Two incomplete juveniles at later stages of development have also been discovered: the estimated length of their dermal armour comprises 26 mm (Fig. 4.46.) and 38 mm (Fig. 4.47. A), respectively. As the squamous part comprises about the same length as the whole dermal armour, then the total estimated length of the body of the oldest young in the studied material could have reached nearly 80 mm.

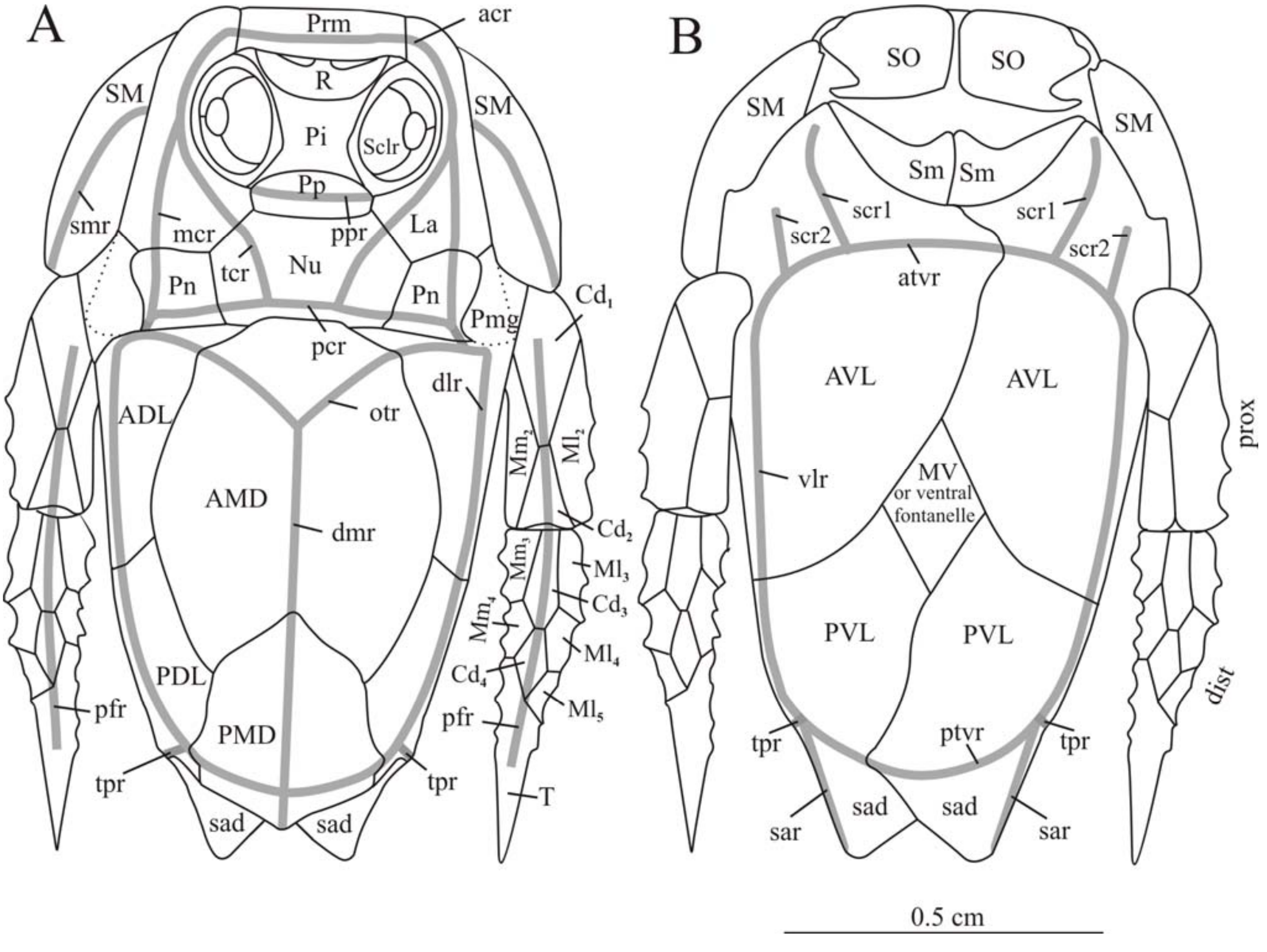


Fig. 4.4. Reconstruction of juvenile of *Asterolepis ornata*. The 2nd stage of ontogeny. Grey solid lines indicate the ridge system. Mainly based on the specimen LDM 260/87, part and counterpart (see Fig. 4.18.). **A,** dorsal side. **B**, ventral side. Anatomical abbreviations in the appendices No 1.

4.4. att. Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija. Otrā ontoģenētiskās attīstības stadija. Pelēkās līnijas iezīmē valnīšu sistēmu. Pārsvarā izmantotas parauga LDM 260/87a un 260/87b abas puses (sk. Fig. 4.18.). **A,** mugurpuse. **B**, vēderpuse. Apzīmējumu saraksts pielikumā Nr. 1.

**General proportions.** There are remarkable differences in body proportions during the growth of the dermal armour (Upeniece, Upenieks, 1992; Upeniece, 2001; Upeniece, 2006). As in the recent fishes, the main difference of body proportions between juvenile and adult individuals results in the rates between the relative size of the orbit and the head to the total body length (Fig. 4.3.). Like most juvenile gnathostomes, the young individuals of *Asterolepis* have large eyes, a large head, longer pectoral appendages etc. (Fig. 4.4.; Table 4.1.).

The general proportions are as following:

1. The head-shield in juveniles accounts for approximately 1/3 of the mid-dorsal length of the body armour while in adults it comprises 1/5.
2. The sclerotic bones in juveniles are considerably larger and orbital fenestra occupies less than 1/3 from the head shield. In adults the orbital fenestra accounts for 1/4 to 1/5 of the length of the head shield, as it is seen in the specimens figured by Lyarskaya (1981, figs. 64. and 65., respectively).
3. The caudal part of juveniles comprises about half of the whole fish length. In adults it comprises 1/3 (Lyarskaya, 1981, p. 119) or less than half (Ivanov *et al*., 1996, fig. 4A).
4. The widest area of the trunk shield in juveniles appeared at the level of the processus brachialis; in adults it emerged in the middle of the trunk (Upeniece, Upenieks, 1992, figs. 2, 3).
5. The pectoral fins in juveniles reach the posterior end of the trunk shield. The ratio of the pectoral fin length is one dorsal armour length in juveniles, and two-thirds in adults, respectively.
6. The length of the distal segment of the pectoral fin, in contrary to that in adult *Asterolepis ornata*, is greater than the length of the proximal segment; ratio length of proximal segment/length of distal segment is 0.57-0.88, but with the growth of the fish they tend to become more uniform in the length: in the older juvenile ratio reaches 0.9.

Table 4.1. Comparison of the proportions of *Asterolepis ornata* body in juveniles and adults (Upeniece, Upenieks, 1992, Table 1, with modifications)

4.1. tabula. Ķermeņa proporciju salīdzinājums bruņuzivju *Asterolepis ornata* mazuļiem un pieaugušajiem īpatņiem (Upeniece, Upenieks, 1992, Table 1, ar izmaiņām).

| *Asterolepis ornata* | orbital fenestra / head shield | head shield / whole dermal armour* | whole dermal armour / squamous part | pect.fin / trunk shield | proximal / distal segment of the pect.fin |
|---|---|---|---|---|---|
| juveniles | (0.32-0.45) | (0.33-0.43) | 1 | 1 | 0.57-0.88 |
| adults | (0.20-0.26) | (0.15-0.21) | 1 | 0.67 | 0.83-0.99 |

* the whole dermal armour length corresponds to the length of the head shield + the length of the dorsal wall of the trunk armour.

### 4.1.3. Ridge system

The prominent external ridge system is extremely well developed in juveniles in early growth of the dermal armour, giving strength to the dermal armour when the lamina of bone was very thin (Fig. 4.4.). It is developed alongside the ossification lines of the head and trunk armour plates, and pectoral fin plates. The ridge system is more remarkable in the earliest stages of the ontogeny: the number of ridges decreased ontogenetically and gradually weakens and slowly diminishes in the oldest known juveniles, when the thicker three-layered bone is fully formed (Figs. 4.46.; 4.47. A). The ridge itself is stout and comparatively high, superficially resembling fold in the cross section.

Ridges run along the margins of the dorsal, ventral and lateral walls, as well as the posterior apperture of the trunk-armour. Numerous ridges are developed on the head-shield. In adults the ridges on the head-shield are not remained at all. The ridge system in juveniles consists of the following ridges (Figs. 4.4.; 4.5.; 4.6.):

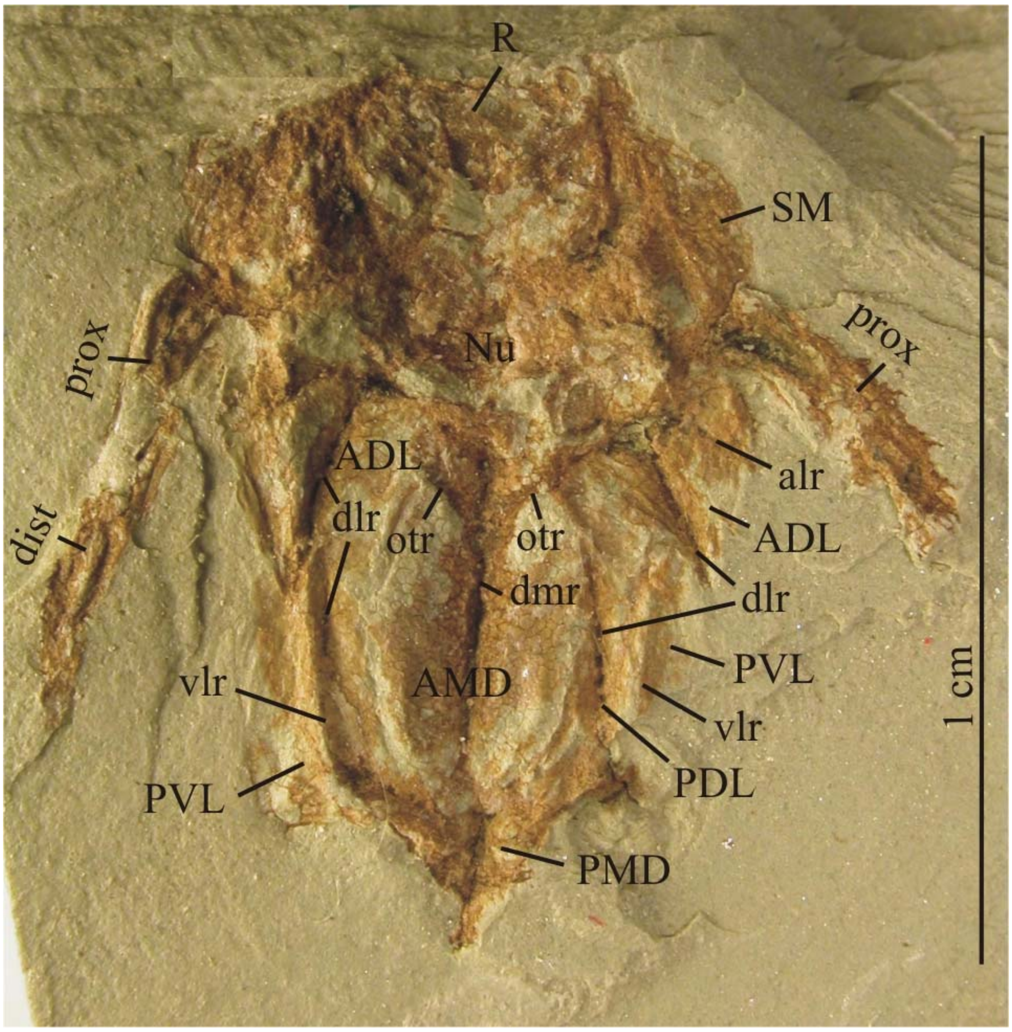


Fig. 4.5. Juvenile individual of *Asterolepis ornata* LDM 260/13a, visceral view of the dorsal wall. Upper Devonian, Frasnian, Lode Fm., Latvia, Liepa (Lode) pit.

4.5. att. Bruņuzivs *Asterolepis ornata* mazulis LDM 260/13a, galvas vairoga un muguras sienas bruņu plātņu iekšskats. Augšdevons, franas stāvs, Lodes svīta, Latvija, Liepas (Lodes) karjers.

1. Longitudinal, transverse and diagonal ridges on the head shield.

From the nuchal plate two diagonal ridges - the transverse cephalic ridges (tcr) branch out on both sides towards the lateral margins of orbital fenestra (Fig. 4.4. A). The marginal cephalic ridge (mcr) in the paranuchal plate proceeds towards the lateral margins of the orbital fenestra. Further forward the anterior cephalic ridge (acr) bends round along the orbital fenestra from its lateral and anterior side. The postpineal ridge (ppr) crossed transversely the Pp plate. The high walls of the orbital fenestra appeared further laterally to it. The posterior margin of the head-shield has transverse posterior cephalic ridge (pcr), which bends down on the posterior lateral corners of the paranuchal plate (Pn) and further cannot be traced. The submarginal ridge (smr) streatches slightly diagonally over the SM plate from its` posterior corner up to the level of the infraspiracular notch of the La plate. The ridge does not been connected with the adjacent ridges.

2. Longitudinal and diagonal ridges on the dorsal wall of the trunk shield.

Dorsal median ridge of the AMD, PMD plates (dmr) stretches along their middle parts, dividing the plates in two symmetrical laminae. The both dorsolateral ridges of the ADL and PDL plates (dlr) mark off the dorsal wall from the lateral walls, as well as divide the mentioned plates into the dorsal and lateral lamina. The anterior lateral ridge of the ADL lateral lamina of the plate; further it has no continuation on the PDL plate (Fig. 4.19.). The plate (alr) stretches from the level of the processus obstans (pro) diagonally across the both oblique transverse ridges of the AMD plate (otr) stretches diagonally from the tergal angle on the *dmr* to the direction of the processus obstans (pro) of the each ADL plate, and there join to the *dlr* and *alr* ridges. The posterior transverse dorsal ridge on the posterior part of the dorsal wall (ptdr) joined with the dorsolateral ridge (dlr) at the level of the posterior transverse lateral ridge (ptlr).

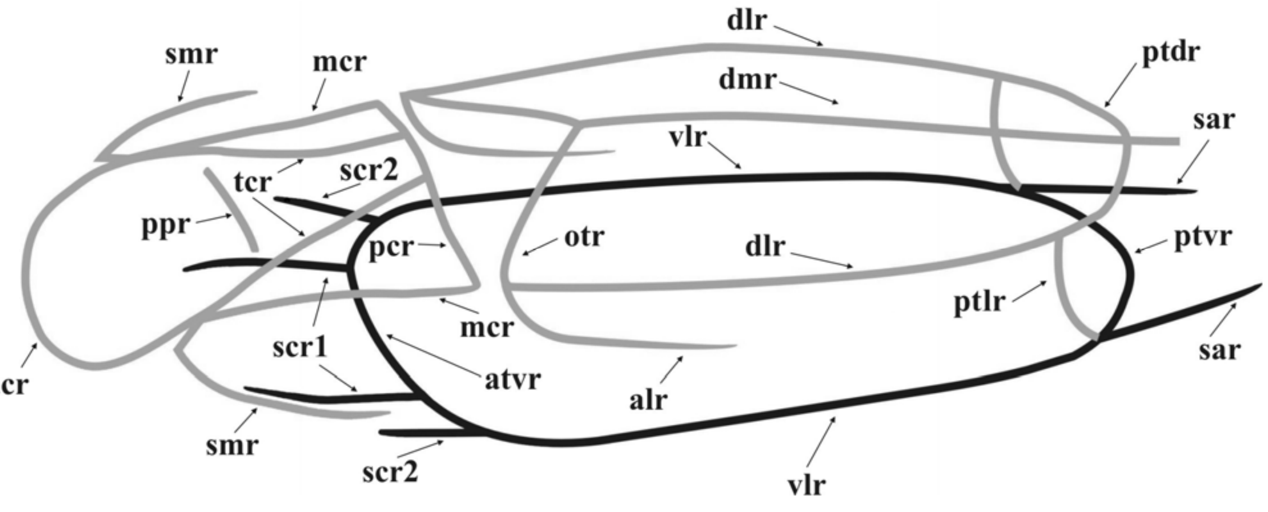


Fig. 4.6. Ridge system of juvenile *Asterolepis ornata*. Grey lines designates those of the head-shield and dorsal wall of the trunk armour; black lines designates those of the ventral wall of the trunk armour. Abbreviations in appendices No 1.

4.6. att. Bruņuzivs *Asterolepis ornata* mazuļa valnīšu sistēma. Pelēkās līnijas ir galvas vairoga un rumpja dorsalās puses valnīšu sistēma; melnās līnijas – ventrālās puses valnīšu sistēma. Apzīmējumu saraksts pielikumā Nr. 2.

3. The longitudinal and transverse ridges of the ventral wall of the trunk shield. The ventrolateral ridge of AVL and PVL plates (vlr) mark off the ventral wall from the laterall walls. The anterior transverse ventral ridge of AVL plates (atvr) mark off the subcephalic part from the ventral side, and posterior transverse ventral ridge of PVL plates (ptvr) mark off the subanal division (sad) from the ventral side. Two pairs of additional ridges on the subcephalic part of the AVL plates (scr1, scr2) stretch to the direction of the antero-mesial corner (am) and to the level of the antero-lateral corner (al), respectively. There is additional ridge on the subanal division of the each PVL plate (sar) as well.

4. The posterior transverse lateral ridges (ptlr) on the lateral walls join the dorsolateral ridge (dlr) with the ventrolateral ridge (vlr). Hence several ridges encircle the whole posterior opening of the trunk armour: *dlr*, *ptlr*, and *ptvr*.

5. The longitudinal ridge on the pectoral fins (pfr) stretches along the middle part of the both segments, proximal and distal ones. Ridges are well visible on the dorsal side of the pectoral fins, whereas their presence on the ventral side is not clear.

The majority of the above mentioned ridges were not described previously for antiarchs up to now. Therefore, new terms for them are introduced for juveniles of *Asterolepis*: 1) of the head-shield (acr, pcr, mcr, tcr, ppr, smr); 2) of the trunk armour (atvr, ptvr, ptdr, alr, scr1, scr2, sar, ptlr).

There are only more or less marked dorso median (dmr), dorso lateral (dlr) and ventro lateral (vlr) ridge in adults of *A.ornata* (Gross, 1931, Fig. 10; Lyarskaya, 1981, fig. 84; Pl. XIII). But, for example, the mentioned ridges are more remarkable in related antiarch *A.radiata* (Karatajūte-Talimaa, 1963, fig. 48) and well known in other antiarchs. In adults the ridge itself is comparatively very low, and convex in the cross section.

### 4.1. 4. Head shield

**General shape.** The head-shield is in its general shape much as in adults of *A.ornata*, it is convex and trapezoidal, and its` width is slightly greater than its length (Figs. 4.4.; 4.9. F). Different configuration has the posterior margin of the head-shield. In juveniles it is slightly concave, in adults – slightly convex. Slightly different is the position of the postmarginal plate in juvenile individuals: the medial margin of it contacts in the full length with the paranuchal plate (Fig. 4.3.).

The head-shield is arched both longitudinally and transversely (best seen in the specimen LDM 260/152). The maximal width is across the nuchal region (Figs. 4.2.; 4.4.), surpassing the length as in other asterolepids. The preorbital area is only slightly arched. It accounts for about 1/2 of the postorbital area as in the adults. In several cases the head-shield plates are detached, revealing the serratiform sutural connections between the plates covering endocranium.

Juveniles in the earliest growth stages do not exhibit preserved traces of the infraorbital sensory line groove of the head-shield, which is well developed in adults and had been initially developed in the oldest known juvenile individuals as well. Juveniles possess a well-developed ridge system, mentioned above. The system of ridges, most probably, strengthened the cranial roof in early stages of ontogeny.

The **orbito-nasal cavity** (orbital fenestra) is of the shape characteristic of the genus (Fig. 4.9. E, F). The suborbital fenestra is remarkably smaller than the orbital fenestra, as in adults of *A.ornata*.

The orbito-nasal cavity in juveniles is large (Fig. 4.4. A), and it occupies about 1/3 to almost a half of the length of the skull roof (ratio 0.32-0.45). In adults the orbito-nasal cavity is remarkably smaller (Fig. 4.3. A) and takes up about 1/4, respectively (Lyarskaya, 1981, figs. 20., 63.-2, 64.). Hereby the preorbital and postorbital areas of the head-shield had been enlarged significantly during the ontogeny. The width of the orbital fenestra during the ontogeny changes only slightly: the ratio of width of the head shield /width of the orbital fenestra ranges from 1.24 to 1.50.

The anterior margin of the orbital fenestra is almost straight; the posterior one is convex, - due to different shape of the postpineal plate in juvenile and adult individuals (Fig. 4.3.). The anterior (acr) and transverse (tcr) cephalic ridges are developed along the anterior and lateral margins of the orbito-nasal cavity. The postpineal ridge (ppr) longitudinally divides the postpineal (Pp) plate into anterior and posterior parts (Figs. 4.2.; 4.4.; 4.9. D,E). In adults the ridges on the head-shield are not observed at all.

The head-shields usually lack preserved postmarginal plates (Pmg) due to their farthermost location and to narrow connection area with the neighbouring plates (Fig. 4.3.). The single detached Pmg plate has been well preserved only in one specimen, described below.

The width/length index of the lateral plate across the postmarginal corner ranges from 1.00 to 1.06. There, without the postmarginal plates (in most of the specimens), the width of the head-shield is equal to the length of it (Fig. 4.2.). In slightly older juvenile individual (LDM 260/152) it comprises 1.13. The latter mentioned specimen is the only one available specimen for the estimated breadth/length index of the head-shield (due to the preserved right postmarginal plate, situated 4 mm beside of the place of origin). There the estimated breadth of the head across the posterior lateral angles of the Pmg plates has reached 11.0 mm; therefore the estimated breadth/length index of the head-shield is 1.2. In adults that index comprises 1.6, respectively (Lyarskaya, 1981, figs. 61., 62., 63.-2). So, with the growth of the individual the head-shield becomes proportionally wider.

The rostral margin of the head-shield in juveniles is seldom preserved due to commonly deformed premedian plate (Prm). The rostral margin is slightly convex with a small concavity or notch in its middle part, as in adults (Lyarskaya, 1981, figs. 20., 63.-2).

The lateral margins of the head-shield in juveniles are almost straight along their length. There is a small concavity in the level of orbital fenestra, possibly for the spiracular foramen (specimens LDM 260/266, 260/382). Some specimens exhibit a small convexity immediately behind the spiracular opening (Fig. 4.9. D). The obstantic margin is preserved only in older juveniles. It stretches vertically on the posterior-lateral margin of the paranuchal plate (LDM 260/152b).

The anterior margin is about twice (2.0-2.4) as narrow as the posterior one (in adult of *Asterolepis ornata* about three times). The median part of the posterior margin formed by the Nu plate is rather variable. The depression between the Pnu and Pmg plates is not developed.

Other prominent structures are the paramarginal and post-orbital cristae, which delineate the otico-occipital depression. This depression in juveniles is seemingly lower than in subadults (LDM 43/450). The depression is of fairly uniform breadth throughout its length as it is characteristic for *Asterolepis* (Stensiö, 1948, p. 53).

## Head-shield plates

**Premedian** (Prm) plate usually appears deformed or fell out, and therefore rarely is well preserved (Fig. 4.7.). The length of the plate in juveniles comprises 0.30-1.40 mm, in adults 18.0-35.5 mm. The length/breadth ratio considerably changes during the growth: in juveniles it gradually increases from 0.19 in smallest one to 0.36 in advanced ones, and in adults it comprises 0.43-0.83 and therefore could be variable feature (appendix 2.1.). Nevertheless the Prm plate in juveniles and adults is difficult to compare at all due to differences in the shape and structure (Figs. 4.7.; 4.9. F).

The anterior margin is about of the same length as posterior one; it is similarly to that in adults. An anterior notch (an) is developed on the anterior margin in juveniles as in adults (Fig. 4.7.). The posterior margin of the plate is variable: straight or strongly concave. The paranasal process (pr) of the posterior margin in adults presumably could be the same, marked for juveniles. The distance between two paranasal processes in juveniles is relatively longer than in adults. The middle part of the plate is variable: it is the narrowest one, or the length of the plate is about the same in its` middle and lateral parts.

The Prm plate bears an anterior cephalic (acr) ridge (Fig. 4.4.). In adults no ridges on the head-shield are observed. Adults bear the remarkable infraorbital sensory line ($ifc_1$), not seen in juveniles. The sutural connections with the adjacent La, SO, R plates in juveniles are of overlapped type. The Prm and rostral plates (R) have a most weakly developed ornament to compare with that of all plates forming the central dorsal head-shield and trunk-shield. The ornamentation of the plate is reticular, in adults appeared radially directed tubercles (Fig. 4.7.).

The orbito-nasal cavity bears the following dermal bones: rostral (R) and pineal (Pi) plates, and sclerotic bones (Sclr) of the eyeball.

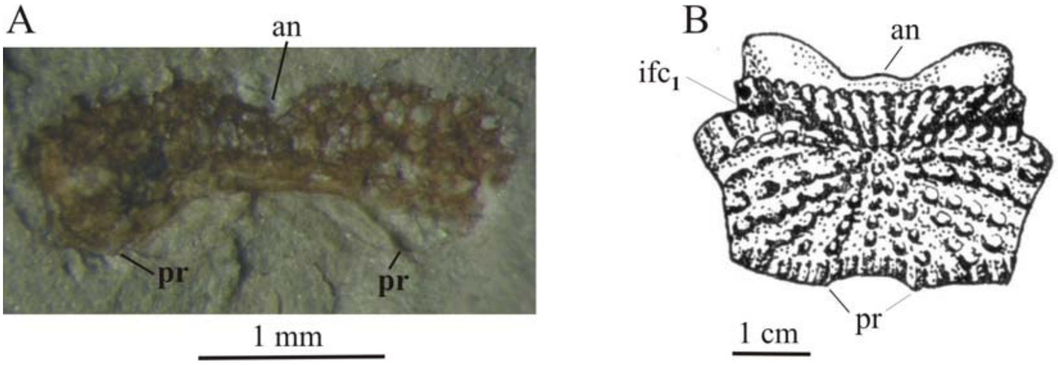


Fig. 4.7. Praemedial plate (Prm) of *Asterolepis ornata*. **A**, of juvenile individual, LDM 260/374a. **B**, of adult individual (Gross, 1931, Pl. IV, Fig. 9).

4.7. att. Bruņuzivs *Asterolepis ornata* priekšējais nepāra kauls (Prm). **A**, mazulim, LDM 260/374a. **B**, pieaugušam indivīdam (Gross, 1931, Pl. IV, Fig. 9).

**Rostral** (R) plate (Fig. 4.8. D,E) is very thin and therefore mostly exhibits only the dorsal and visceral surfaces, in one case the plate is partly seen from the lateral view. The anterior margin of the rostral plate (Figs. 4.8. E,D; 4.9. A) only slightly resembles that of the adult (Fig. 4.8. G). The posterior margin is fairly straight in juveniles; in adults it is nearly convex. Anterior process (ap) of the plate is straight (Figs. 4.8.; 4.9. A), in adults – fan-shaped (aop).

The length of the plate in juveniles comprises 0.45-0.65 mm, in adults 6.0-7.1 mm. The length/width ratio of the rostral plate in juveniles comprises 0.34-0.45; in adults - 0.27-0.38 (appendix 2.2., a/b). The ornamentation of the plate is fine-meshed, in adults – lines of fine-dotted tubercles.

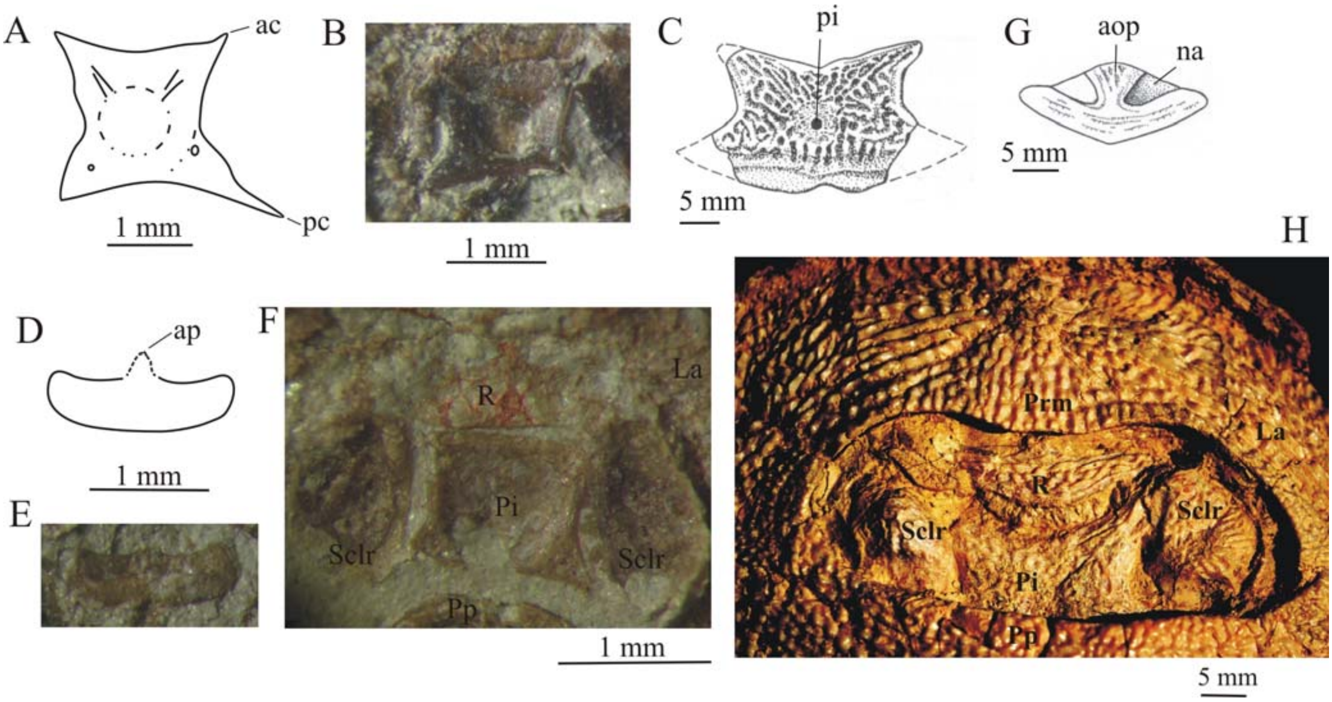


Fig. 4.8. Dermal bones of the orbito - nasal cavity of juveniles and adults of *Asterolepis ornata* **A, B** Pineal plate (Pi) of juvenile. A, LDM 260/152a, in visceral view. B, LDM 260/118a, in visceral view. **C**, Pineal plate (Pi) of adult (Lukševičs, 2001, Fig. 3E), in external view. **D-E,** Rostral plate (R) of juvenile. LDM 260/59a, in visceral view. **F**, Orbito-nasal cavity of juvenile. LDM 260/266a, in visceral view. **G**, Rostral plate (R) of adult (Lukševičs, 2001b, Fig. 5A), in external view. **H**, Orbito-nasal cavity of adult. UP 10/1-1.

4.8.att. Orbito - nazālā dobuma kompleksa kauli bruņuzivs *Asterolepis ornata* mazuļiem un pieaugušajiem īpatņiem. **A, B** Pineālais kauls (Pi) mazulim. A, LDM 260/152a, iekšskats. B, LDM 260/118a, iekšskats. **C**, Pineālais kauls (Pi) pieaugušam īpatnim (Lukševičs, 2001, Fig. 3E), ārskats. **D-E,** Rostrālais kauls (R) mazulim LDM 260/59a, iekšskats. **F**, Orbito-nazālais dobums mazulim LDM 260/266a, iekšskats. **G**, Rostrālais kauls (R) pieaugušam īpatnim (Lukševičs, 2001b, Fig. 5A), ārskats. **H**, Orbito-nazālais dobums pieaugušam īpatnim. UP 10/1-1.

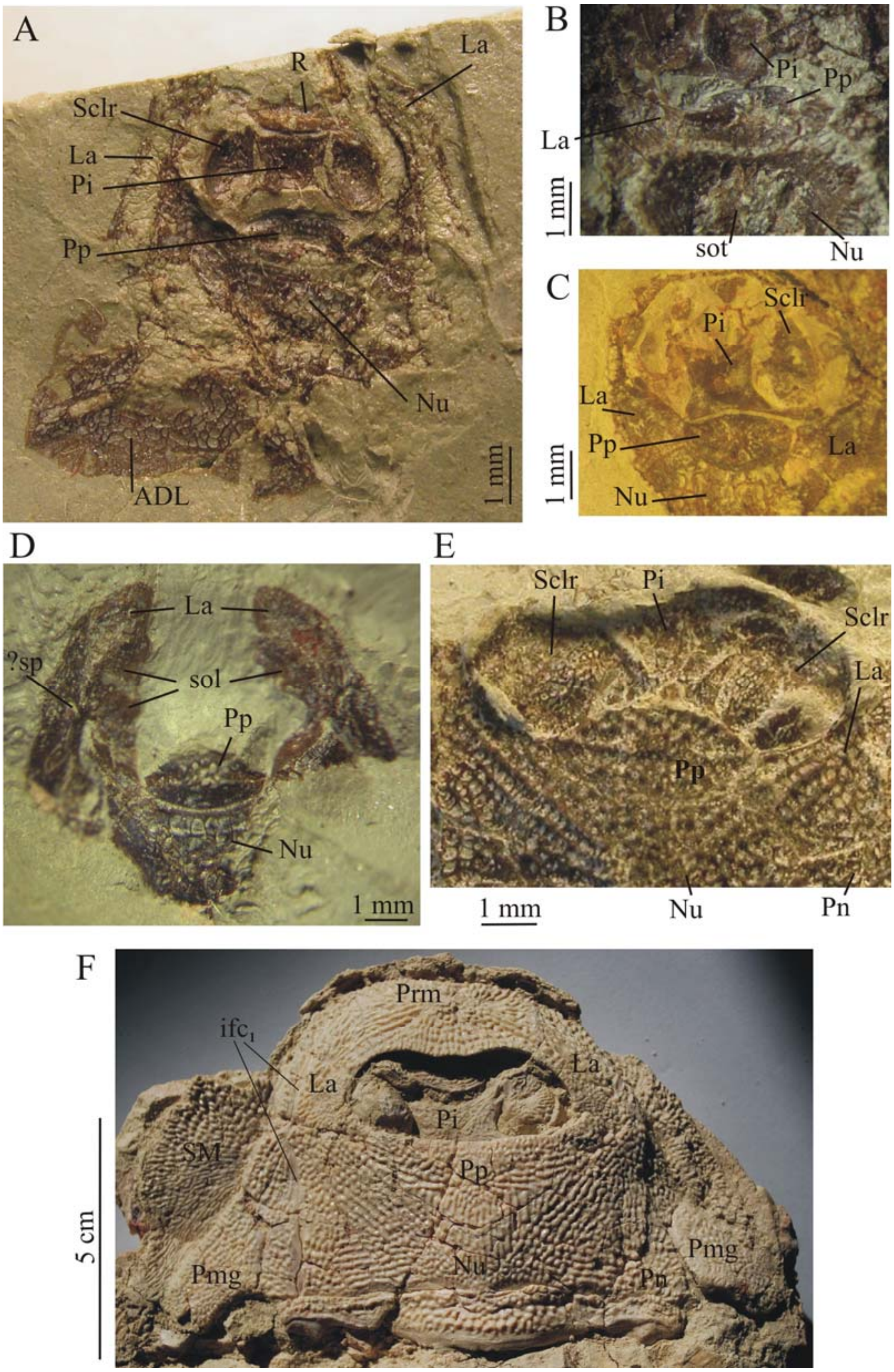


Fig. 4.9. Dermal armour plates of the head-shields of juvenile *Asterolepis ornata* (**A-E**). A, LDM 260/82a, in visceral view. B, LDM 260/150a, in visceral view. C, LDM 260/152a, in visceral view. D, LDM 260/299a, in visceral view. E, The orbito-nasal cavity and adjacent plates of the advanced juvenile, LDM 260/78, in dorsal view. **F**, Armour plates of the head of adult *Asterolepis ornata* UP 10/1-1, in dorsal view.

4.9.att. Bruņuzivs *Asterolepis ornata* mazuļa galvas vairoga dermālās bruņu plātnes (**A-E**). A, LDM 260/82a, iekšskats. B, LDM 260/150a, iekšskats. C, LDM 260/152a, iekšskats. D, LDM 260/299a, iekšskats. E, Orbito-nazālais dobums un blakus esošās galvas vairoga bruņu plātnes lielākam mazulim, LDM 260/78, dorsālais skats. **F**, Pieaugušas bruņuzivs *Asterolepis ornata* galvas bruņu plātnes UP 10/1-1, dorsālais skats.

**Pineal** (Pi) plate, as compared to that in adult of *Asterolepis ornata*, is more arched and with well-marked elevated pineal pit (Fig. 4.8. A, B). The pineal plate possesses tapered corners. The postpineal (Pp) and the lateral (La) plates usually overlapped the posterior margin of the pineal plate.

The length of the plate in juveniles comprises 0.95-2.00 mm, in adults 11.5-13.0 mm. The shape of the pineal plate in juveniles (Fig. 4.9. A,B,F) is near to quadrate (if tapered corners are not taken into account; appendix 2.3., $a_1/b_1$), contrary to that in adults (Fig. 4.8. C). The posterior corners (pc) in advanced juveniles are longer (as in adults) and more tapered than anterior ones (ac) (Figs. 4.8. A; 4.9. C). In adults the pineal plate is trapezoidal in the shape and is broader than it is long (Fig. 4.8.C). The length/width ratio of the Pi plate in juveniles changes from 0.63-0.79 to 0.41-0.50 in adults (appendix 2.3., a/b).

The anterior margin is shorter than the posterior one, as in adults; lateral margins are only slightly concave contrary to that in adults, where they are strongly concave. In advanced juveniles (Figs. 4.8. A; 4.9. C) all margins are concave. In adults almost all margins are concave, except the posterior one, which is convex. This distinction is due to the different shape of the anterior margin of the postpineal plate in juveniles and adults.

A small pineal foramen (pi) pierces the bone as in adults, as well as additional small foramens can be seen in the posterior lateral part of the plate (Fig. 4.8. A), which probably could be interpreted as foramens for blood-vessels.

The outer surface is covered with reticulate ornamentation. An advanced juvenile exhibit an unornamented area, developed along the both lateral margins of the plate, as in adults (Fig. 4.8. C). It is divided from the ornamented area by the sharp and arched ridges, stretching from the anterior corners to the posterior ones (Fig. 4.9. E), hence having radiating appearance. Radiating ridges on the Pi plate are known also for *Pterichthyodes milleri* (Hemmings, 1978, fig. 5 B) and an `asterolepidoid` (Young, 1984b, fig. 2 B). No radiating ridges are known in adults of *Asterolepis ornata* (Fig. 4.8. C), although there is the more or less radiating ornament developed in the corresponding area (Fig. 4.8. C). The same radiating ornament is seen on the pineal of *Asterolepis radiata* (Karatajūte-Talimaa, 1963, Pl.10, fig.2).

**Sclerotic bones** (Sclr) are dermal ossifications covering the eyeball and forming the sclerotic capsules. They are rare to be well seen (Figs. 4.2.; 4.8. F; 4.9. A,C, E; 4.45. A) due to their quite fine structure and deformation of the orbito-nasal cavity during the compaction of sediments. Therefore mostly the only one of them is exposed, the mesial one. The shape of the mesial sclerotic bone is fairly oval (Figs. 4.9. A,C; 4.10.). All three sclerotic bones are convex as in adults (Fig. 4.8. H); they are covered with the fine-meshed to reticular ornament.

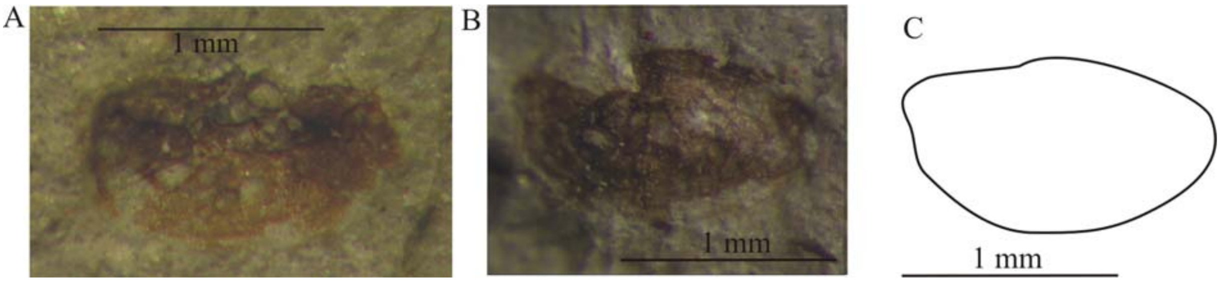


Fig. 4.10. Sclerotic bones (Sclr) of the eyeball of juvenile *Asterolepis ornata*. **A,** LDM 260/403, in visceral view. **B, C,** LDM 260/87a, in visceral view.

4.10. att. Acs ābola sklerotiskie kauli (Sclr) bruņuzivs *Asterolepis ornata* mazulim. **A,** LDM 260/403, iekšskats. **B, C**, LDM 260/87a, iekšskats.

**Postpineal** (Pp) plate in juveniles considerably differs from that in adults, having a fusiform shape (Fig. 4.11. A-C). Anterior margin is remarkably convex, hence the shape of the posterior margin of the orbital fenestra changes significantly during ontogeny (Figs. 4.4.; 4.9.). In adults the anterior margin is almost straight (Fig. 4.11. D), hence the posterior margin (Fig. 4.3. A) of the orbital fenestra is almost straight too (Lyarskaya, 1981, fig. 20).

The plate is well preserved both in articulated and disarticulated juvenile individuals. A transverse ridge (ppr) is crossing the Pp plate at the level of the orbital fenestra (Figs. 4.2.; 4.4. A; 4.11. A). In the smallest known specimen this transverse ridge occupies almost all the area of the plate (Fig. 4.43. A).

The shape of the Pp plate has been changed farther during the ontogeny: there are distinctive lateral process developed in the first stage of ontogeny (specimen LDM 260/200); then the small lateral margins had been developed from that process (Fig. 4.2.). The length of it comprises only 0.1 mm. In advanced juveniles the lateral margins comprised 0.40-0.65 mm (Figs. 4.9.C-E; 4.11. B,C), and in the largest juvenile individual it comprises 0.8 mm in length (LDM 260/10), having somewhat similarity to that in adult individuals (Gross, 1931, Pl. IV, Fig. 1). In adults the lateral margins are considerably longer, the posterior margin possess the well-marked posterior process not visible in juveniles (Fig. 4.11. D). The length of the lateral margins in adults ranged from 9.7 to 13.5 mm. The ratio the length of the plate/the length of the lateral margin decreases remarkably during the growth: from 8.00 in smaller juveniles to 2.00-3.13 in advanced ones, reaching 1.46-2.03 in adults (appendix 2.4., a/c).

The length of the plate comprises 0.55-2.50 mm in juveniles, 11.2 mm in subadult one, and 15.0-20.5 mm in adults. The length/width ratio of Pp plate has been changed only slightly during the growth: it comprises 0.39-0.45 in smallest juveniles, 0.46-0.50 in advanced ones, 0.53-0.64 in adult individuals (appendix 2.4., a/b). Consequently, the shape of the Pp plate had been changed from slender and fusiform in juveniles to stout in the appearance in adults.

The visceral side in advanced juveniles exhibit marked pits. The median ridge (mr) between them (Fig. 4.11. C) is well developed as in adult individuals (Fig. 4.32. F). The postorbital crista (cr.pto) continued on the Pp plate from the both neighbouring La plates. The ornament of the plate in smaller juveniles is fine-meshed and reticular, in advanced ones – tubercular (Fig. 4.46.): tubercles are located in several rows. There is a serratiform connection type with the Nu plate (Fig. 4.32. A, C).

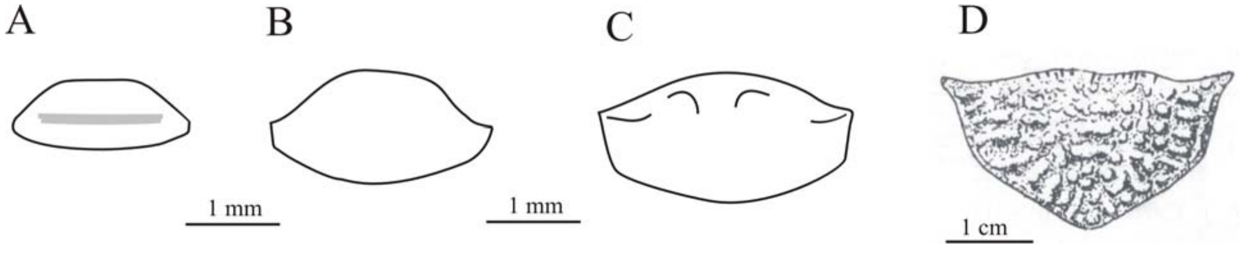


Fig. 4.11. Postpineal plates (Pp) of *Asterolepis ornata*. **A-C**, of juveniles. **A**, LDM 260/87b, in dorsal view. **B**, LDM 260/299. **C**, LDM 260/152a, in visceral view. **D**, of adult (Karatajūte-Talimaa, 1963, Fig. 23-2).

4.11. att. Bruņuzivs *Asterolepis ornata* pakaļējais pineālais kauls (Pp). **A-C**, mazuļiem. **A**, LDM 260/87b, dorsālais skats. **B**, LDM 260/299. **C**, LDM 260/152a, iekšskats. **D**, pieaugušam īpatnim (Karatajūte-Talimaa, 1963, Fig. 23-2).

**Nuchal** (Nu) plate. The length of the plate comprises 2.1–4.5 mm in juveniles, 10.5-39.2 mm in subadults and adults. The shape of the Nu plate in juveniles is considerably different from that in adults and exhibits a sequence of gradually changes during the growth (Fig. 4.12.).

The width of the plate is about twice as the length in adults (Lyarskaya, 1981, p. 103). In the smallest juveniles (Fig. 4.12. A,B) this ratio comprises 0.8; in the little larger ones it decreased up to 0.7 (Fig. 4.2.) and up to 0.6 in advanced ones (Fig. 4.12. E,F). In the largest ones (Fig. 4.46.) the plate becomes similar in proportions to that in adults (appendix 2.6., $a_0$/b).

The anterior margin of the Nu plate bears a very shallow postpineal depression (dpp) (Fig. 4.12.A-D), becoming gradually deeper in the advanced ones (ibid.: E,F). It becomes remarkably deep, triangular and sharp edged in subadult and adult individuals (ibid.: H,J,K), sometimes with the small notch for the posterior corner of the Pp plate. The convexity of the posterior margin gradually decreased during the growth.

The Nu plate exhibits serratiform connections with the neighbouring Pnu, La and Pp plates in juveniles (Figs. 4.12. A-F; 4.32. A-E). The overlapped area for the postpineal (Pp) plate is well remarkable: narrow and gently sloping in juveniles, it becomes fairly wide (Fig. 4.12. J,K), steep and with sharp notch in adult individuals (Gross, 1931, Pl. IV, fig.6). In adults the Nu plate has a gentle conjunction with the adjacent plates.

The plate bears remarkably developed ridges: the transverse cephalic (tcr) and the posterior cephalic (pcr) ridge. They are continuing to the adjacent armour plates: *tcr* to the both La plates, and *pcr* to the both Pn plates. The configuration of the *pcr* slightly changes during the growth of the individual: from diagonal to transverse (Figs. 4.4. A; 4.12. A,C).

Gradual changes of the shape during the growth of the individual represent the sequence of the following growth (ontogenetic) stages:

1) The plate is nearly roundish in the earliest known growth stage (Fig. 4.12. A, B); only anterior margin is almost straight with very weakly developed depression for the Pp plate (dpp). The anterior corners (ac) had been initially developed. The lateral corners (lc) were not well pronounced yet. The transverse cephalic (tcr) and posterior cephalic ridge (pcr) are very strongly developed, they are directed diagonally almost from the centre of the plate to the corners. Plate is very thin and therefore translucent: only the basal layer of the dermal bone is developed. So, the shape of the Nu plate in the first ontogenetic stage does not resembles that of the adult at all.

2) The second stage is characterised by the following features. The depression for the Pp plate (dpp) becomes more pronounced, although it was rather shallow. The pronounced lateral corners (lc) appear (Fig. 4.12. C,D). The *tcr* and *pcr* ridges have been joined on the central part of the plate (Figs. 4.12.C; 4.32. D,E). The *pcr* ridge grew transversely and divided the Nu plate into the anterior and posterior parts (appendix 2.6: ratio 1/2). There are two depressions (depr) developed behind the *pcr* ridge, separated by a wide median vault (Figs. 4.2.B; 4.32. A,D). The serratiform connections with the adjacent Pp, La and Pn plates are very pronounced: they have been represented the flat serrated structures (Fig. 4.32. A-E). The ornament of the plate is fine-meshed; it is very weakly developed along the posterior margin.

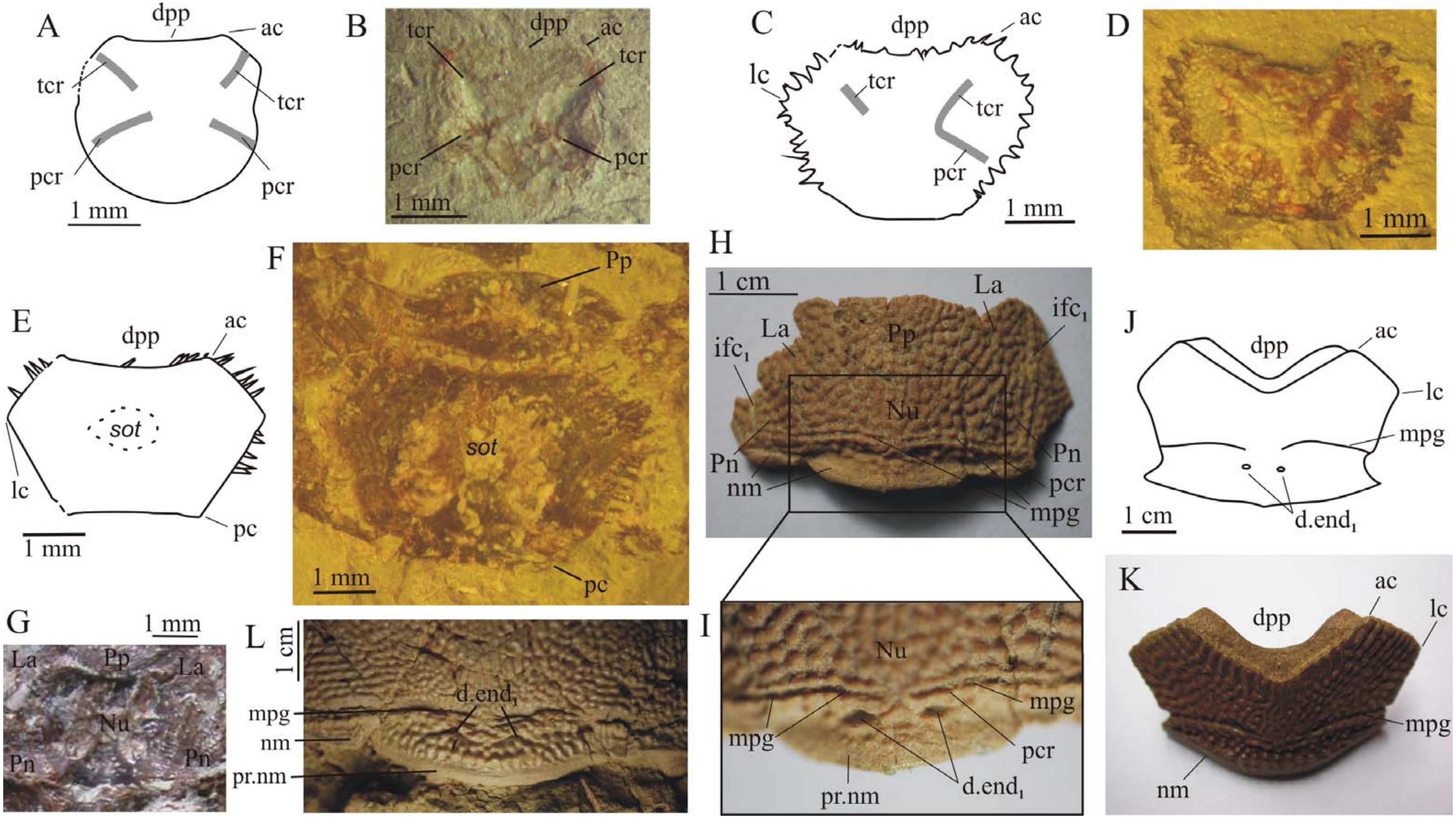


Fig. 4.12. Sequence of development of nuchal plates (Nu) of *Asterolepis ornata* in juveniles (**A-G**), and in subadults and adults (**H-L**). A, B, the 1st stage of ontogeny, Nu in dorsal view. LDM 260/383b. C, D, the 2nd stage of ontogeny, Nu in dorsal view. LDM 260/385a. E, F, the 3rd stage of ontogeny, Nu in visceral view. LDM 260/150. G, the 3rd stage of ontogeny, Nu in visceral view. LDM 260/260. **H-I,** nuchal plate and adjacent armour plates of subadult individual, dorsal side. LDM 43/450. **J-L,** nuchal plates of adult individuals, in dorsal view. J, after Gross (1931, Pl. IV, fig. 6). K, unnumbered specimen LDM. L, posterior part of the nuchal plate. UP 10/1-1.

4.12. att. (iepr.lpp.) Pakauša kaula (Nu) secīga attīstība bruņuzivju *Asterolepis ornata* mazuļiem **(A-G)**, pusaugu un pieaugušiem indivīdiem **(H-L)**. A, B, Pirmā ontoģenētiskās attīstības stadija, dorsālais skats. LDM 260/383b. C, D, Otrā ontoģenētiskās attīstības stadija, dorsālais skats. LDM 260/385a. E, F, Trešā ontoģenētiskās attīstības stadija, iekšskats. LDM 260/150. G, Trešā ontoģenētiskās attīstības stadija, iekšskats. LDM 260/260. **H-I,** pakauša kauls un apkārtējās bruņu plātnes pusaugu īpatnim, dorsālā puse. LDM 43/450. **J-L,** pakauša kauli pieaugušiem īpatņiem, dorsālais skats. J, pēc Gross (1931, Pl. IV, fig. 6). K, nenumurēts paraugs LDM. L, pakauša kaula aizmugurējā daļa. UP 10/1-1.

3) In the third stage the depression for the Pp plate (dpp) remains shallow, but clearly marked in the advanced juveniles (Fig. 4.12. E,F). The anterior (ac), lateral (lc) and posterior corner (pc) were well developed. The supraotic thickening of the head-shield (sot) on the visceral surface is presented (Fig. 4.12.E). The dermal bone has fully developed 3-layer structure. The serratiform connections transformed from flat to roundish in the section. The plate is strongly arched as in adults. The initial development of the obtected nuchal area appears (nm).

4) The shape of the nuchal plate in the forth stage of the development (Fig. 4.46.) tends to be similar to that in adult individuals (Figs. 4.9. F; 4.12. J,K): the posterolateral corners (pc) are already well developed as in adults (Gross, 1931, Pl. IV, figs. 6,7). Behind the transverse *pcr* ridge (Fig. 4.4.A) a posteriorly gently sloping ornamented area is developed: seemingly it extends beneath the most anterior part of the AMD plate (Fig. 4.46.). This area continues posterio-laterally to the neighbouring paranuchal (Pn) plate, where it becomes narrower and disappears near the joint of the Pn plate with the trunk-armour (ADL plate).

The middle pit-line groove (mpg) is initially developed (Fig. 4.46.): it is the first known developed sensory line groove in *Asterolepis ornata* juveniles. In adults it is remarkably developed. There is no good sign of external openings for the endolymphatic ducts (d.end$_1$) in juveniles, which are well visible in subadults and adults (Fig. 4.12. H-L). Plate bears reticularly radial ornament of anastomosing ridges.

5) The area behind the transverse *pcr* ridge lost the ornament and became shorter, as well as steeper with developed longitudinal convexity in the oldest known juvenile individual (Fig. 4.47.). The plate bears radially located tubercules, except the *nm* area.

6) The Nu plate of subadult individual or small-sized adult individual (Fig. 4.12. H, I) exhibits developed unornamented posterior median process (pr.nm) overlapped by the anterior margin of the AMD plate. The plate shows yet preserved *pcr* ridge, which have been diminished later in adults. Backwards the *pcr* ridge dorsal openings of canal for ductus endolymphaticus (d.end$_1$) are located on the *pr.nm*. Some initially developed tubercles are observed backwards of the openings.

7) The area backwards the above mentioned openings has been covered by tubercles in adults (Fig. 4.12. L), hence the obtected nuchal area (nm) becomes narrower.

Two remarkable points mark the changes in the shape of the Nu plate (Fig. 4.12.): 1) the postpineal depression (dpp) gradually has been enlarged from the shallow to the remarkably deep and triangular in adult; the corresponding ratio comprises from 23.00 in the smallest juvenile individual to 6.43 in the advanced one, and up to 3.21 in adults (appendix 2.6., ratio $a_0/a_1$). 2) the posterior part of the Nu plate backwards of the *pcr* ridge has been grew more slowly than the anterior one (appendix 2.6., ratio 3/2).

The ornament of the plate in juveniles changes from the fine-meshed in youngest ones to reticulate in advanced, and to radially arranged tubercules in the oldest ones.

The visceral surface of the Nu plate in two advanced juvenile individuals (LDM

260/150, 260/260) shows diagonally located ridges, directed from the posterior corners to the central part of the plate (Fig. 4.12. G). They are seen in subadult individual (LDM 43/450) also, as well as slightly developed in adults (unnamed, Gross, 1931, Pl. IV, fig. 6).

**Paranuchal** (Pn) plate. The shape of the plate changes during the growth (Fig. 4.13.). The anterior, lateral and mesial margins in juveniles are straight as in adults. The anterior margin has well-developed serratiform connections with the adjacent La plate (Fig. 4.13. B). The postero-lateral part of the plate became more wider during the ontogeny (Fig. 4.13. A,B; appendix 2.7., $b_1$). The shape of the plate in one of the largest juvenile (Fig. 4.46.) exhibit already the similar shape as in adults.

The length of the plate comprises 1.5-2.1 mm in juveniles, and 16.5-25.3 mm in adults. The length/width ratio does not exhibit remarkable changes during the growth: it is slightly below 1.00 in juveniles and in adults (appendix 2.7., a/b).

Two ridges crossed the plate: the marginal cephalic (mcr) and the transverse cephalic (tcr) ridge (Figs. 4.4.; 4.13. A,B). In adults they have not been observed. The infraorbital sensory line (ifc$_1$) is well developed in adults about in the same level as the marginal cephalic ridge (mcr) in juveniles; and the middle pit-line groove (mpg) in adults is about in the same level as the posterior cephalic ridge (pcr) in juveniles. Both sensory lines are noted in one of the oldest juvenile individual (Fig. 4.46.). Obviously they might have been appeared simultaneously in the later ontogenetic stages. The same is visible in the subadult individual also (Fig. 4.13. C,D).

Sutural connections with the adjacent nuchal and lateral plates are of serratiform type; the connection type with the Pmg plate remains unclear.

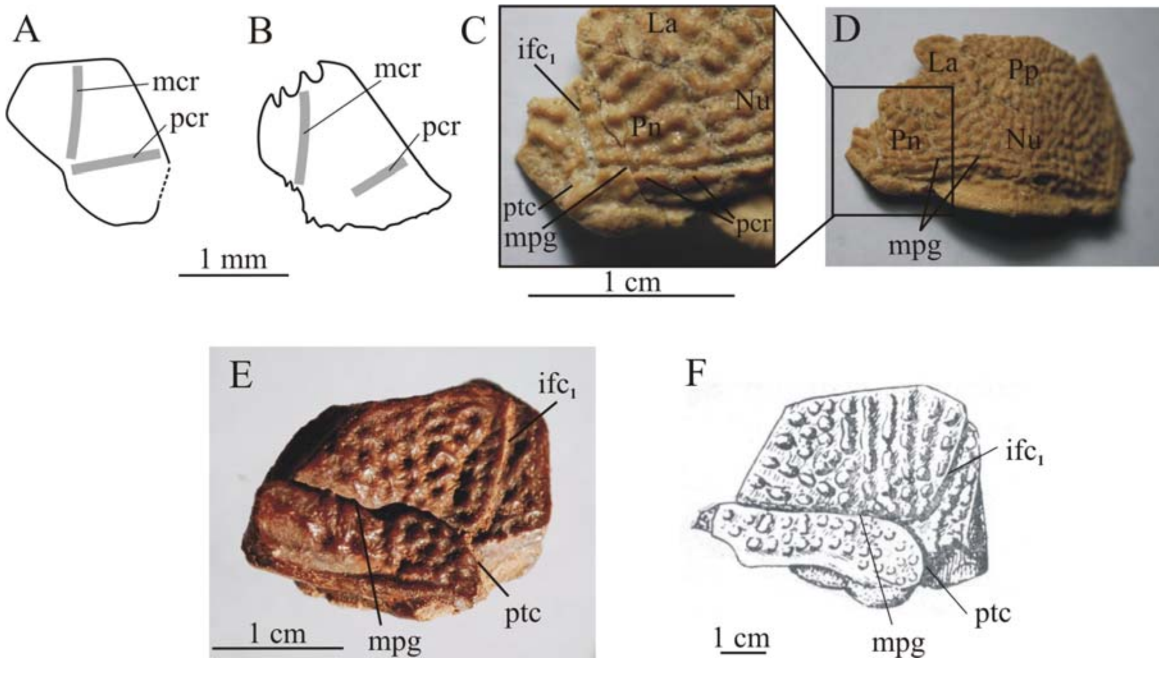


Fig. 4.13. Paranuchal plate (Pn) of *Asterolepis ornata*. **A, B**, of juvenile, left Pn, in dorsal view. A, LDM 260/266. B, LDM 260/193. **C**, **D**, of subadult, left Pn LDM 43/450, in dorsal view. River Gauja, outcrop Katlapi. **E, F**, of adult, right Pn. E, LDM 43/362, in dorsal view. River Gauja, outcrop Ērmaņi. F, after Gross (1931, Pl. IV, Fig. 5).

4.13. att. Bruņuzivs *Asterolepis ornata* sānu pakauša kauls (Pn). **A, B**, mazuļiem, kreisais Pn, dorsālais skats. A, LDM 260/266. B, LDM 260/193. **C**, **D**, pusaugu īpatņiem, kreisais Pn LDM 43/450, dorsālais skats. Gauja, Katlapi. **E, F**, pieaugušiem īpatņiem, labais Pn. E, LDM 43/362, dorsālais skats. Gauja, Ērmaņi. F, pēc Gross (1931, Pl. IV, Fig. 5).

The shape of the **lateral** (La) plate in general is similar to that in adults. The plate has a convex anterior margin as in adults. The posterior and the lateral margins are similar to these in adults. The lateral margin of the La plate overlies the submarginal (SM) plate. The spiracular groove (sp) presumably is preserved in the specimen LDM 260/299 (Figs. 4.9.D; 4.14.D). In adults it is narrow and shallow (Fig. 4.14.F) (Stensiö, 1948, fig. 17).

The anterior part of the mesial margin (amm) (in contact with Prm plate) is variable: it stretches longitudinally or diagonally; it is several times shorter than in adults (Figs. 4.9. D; 4.14.; appendix 2.5., $a/a_3$); in adults the margin is diagonal (Gross, 1931, Pl. IV, Fig.15). The medial part of the mesial margin is long (in adults – relatively shorter) and remarkably concave for the large orbital fenestra. The suborbital lamina (sol) is well developed (Figs. 4.9.D; 4.14. B,F). The posterior part of the mesial margin (pmm) (in contact with the Pp plate) is short in contrary to that in adults (Fig. 4.3.). It became more than twice longer with the growth of the fish: the ratio $a/a_2$ changes from 11.60-6.89 in juveniles to 5.03 in subadult and 4.08-4.96 in adults (appendix 2.5., $a/a_2$).

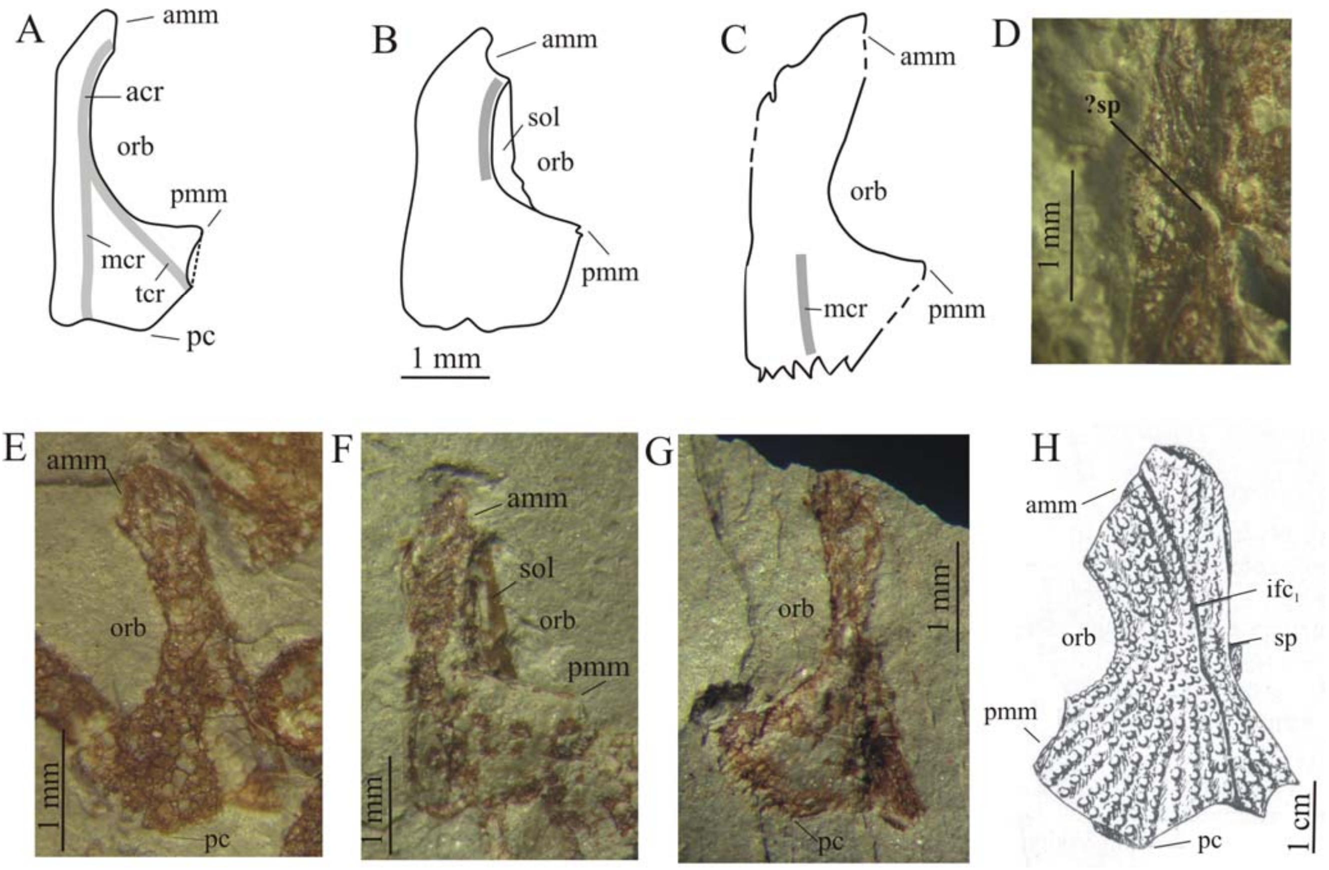


Fig. 4.14. Lateral plates (La) of *Asterolepis ornata*. **A-G**, of juvenile individuals. A, Left La, LDM 260/87b, in dorsal view. B, F, Left La, LDM 260/382a, in dorsal view. C, Left La, LDM 260/193. D, Attachment area to the SM plate, LDM 260/299a, in visceral view (fragment from Fig. 4.9.D). E, Right La, LDM 260/87a, in visceral view. G, Right La, LDM 260/374b, in dorsal view. **H**, of adult (after Gross, 1931, Pl. IV, Fig. 15).

4.14. att. Bruņuzivs *Asterolepis ornata* sānu plātnes (La). **A-G**, mazuļiem. A, kreisā La, LDM 260/87b, dorsālais skats. B, F, kreisā La, LDM 260/382a, dorsālais skats. C, kreisā La, LDM 260/193. D, piestiprināšanās vieta SM plātnei, LDM 260/299a, iekšskats (fragments no Fig. 4.9.D). E, labā La, LDM 260/87a, iekšskats. G, labā La, LDM 260/374b, dorsālais skats. **H**, pieaugušam īpatnim (pēc Gross, 1931, Pl. IV, Fig. 15).

The La plate bears a part the of the head-shield ridge system. The anterior cephalic (*acr*) ridge on the medial edge of the plate is high and narrow; then further backwards two ridges originated from it - a transverse cephalic ridge (tcr) proceeds diagonally backwards to the posterior margin of the nuchal plate, and a marginal cephalic ridge (mcr) longitudinally across the posterior part of the plate stretches to the posterior lateral corner of the paranuchal plate (Figs. 4.2. B; 4.4.; 4.14. A).

The length of the plate in juveniles comprises 2.9-6.2 mm, in subadult specimen 17.6 mm, in adults 34.4-58.0 mm. The length/width ratio of the plate in juveniles and adults do not exhibit remarkable changes (Fig. 4.3.): it is almost twice as long as broad (appendix 2.5: a/b). The plate is relatively narrower at the level of the orbital fenestra, to compare with that in adults (Gross, 1931, Pl. IV, figs.14,15; Stensiö, 1948, fig.17). It is due to the decreasing relative size of the orbital fenestra during the growth of the individual (appendix 2.5., $a/b_1$). So, the ratio between the length of the plate to the width at the level of the orbital fenestra comprises 5.80-4.80 in juveniles, and 3.74-3.28 in adults. The ratio length of the plate/ length of the orbital part changes during the ontogeny (appendix 2.5., $a/a_1$): 1.71 to 2.21 in juveniles, 2.59 in subadult, and 2.71-3.19 in adults. So, in juveniles the length of the orbital fenestra occupies about the half of the length of the La plate, whereas in adults about one third.

Sutural connections with the adjacent postpineal (Pp), nuchal (Nu) and paranuchal (Pn) plates are of serratiform type; whereas with the premedian plate (Prm) is of overlapped type. The dermal articulation between the SM and La plate is supported by a thickened ridge of bone beneath the lateral plate (LDM 260/299). Such small ridge is seen also in adult of *Asterolepis ornata* (Stensiö, 1948, fig.17a). The mentioned contacting area with SM plate has reticularly-radiated ornament (Fig. 4.9.D).

**Postmarginal** (Pmg) plate is very seldom preserved (Fig. 4.15. A,B), as being loosely attached to the head shield (as in adults of *Asterolepis* and in other antiarchs). The mesial margin is more convex than that in adults (Fig. 4.15. C) due to the less pronounced postero-lateral corner (plc). The anterior corner is pointed. The lateral margin is almost straight as in adults.

The maximal width is observed in the middle of the plate as in adults. The length of the plate comprises 2.2-3.0 mm, in adults 23.1-34.0 mm. The length/width ratio in juveniles and adults is about the same: in advanced juveniles it comprises 2.00-2.44, in adults 1.90-2.48 (appendix 2.8.).

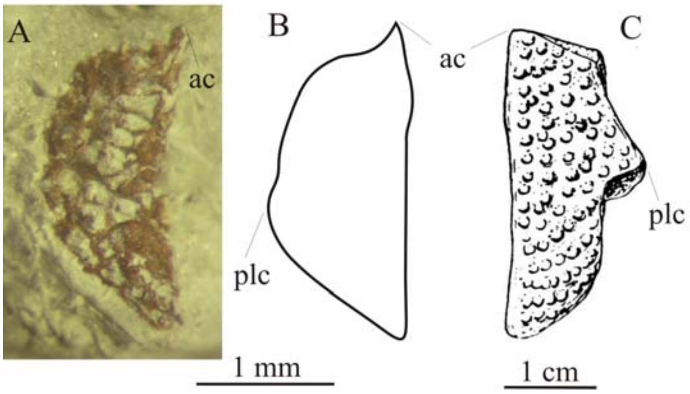


Fig. 4.15. Postmarginal plate (Pmg) of *Asterolepis ornata*. **A, B,** of juvenile, right Pmg, LDM 260/152b, in dorsal view. **C,** of adult, left Pmg (Gross, 1931, Pl. IV, Fig. 2).

4.15. att. Bruņuzivs *Asterolepis ornata* pakaļējās malas plātne (Pmg). **A, B,** mazuļiem, labā Pmg, LDM 260/152b, dorsālais skats. **C,** pieaugušam īpatnim, kreisā Pmg (Gross, 1931, Pl. IV, Fig. 2), dorsālais skats.

**Submarginal** (SM) plate (*operculum* of Stensiö, 1948; Lyarskaya, 1981) is of elongate elliptical shape (Fig. 4.16.) and is about two times (three times in adults) as long as wide. It is well presented in 17 disarticulated specimens. Its' maximum width is across the middle as in adults. In juveniles the SM plate is relatively shorter than in adults: it extends about till the posterior margin of the lateral plate (Figs. 4.2.; 4.4.). In adults the SM plate (Fig. 4.3.) extended till about the level of the posterior margin of the Pmg plate (Lyarskaya, 1981, figs. 20,21) as it is seen also in *Asterolepis scabra* (Nilsson, 1941, fig.3). Therefore the SM plate is shorter than the lateral plate (La) in juveniles unlike to that in adults.

The length of the plate comprises 2.40-4.50 mm. The length/width ratios do not exhibit changes with the growth (appendix 2.9., ratios a/b, $a_1$/b). There is no detached SM plate of adult available for the comparative measurements.

The SM plate is longitudinally convex forming the dorsal and lateral divisions. The shape of SM in juveniles closely resembles that of *Pterichthyodes milleri* (Hemmings, 1978, fig. 5 E-I, Pl. 3, fig.1), as well as of *Sherbonaspis hillsi* (Young, Gorter, 1981, fig. 14). The latest possess an external ridge, similar to that, but much shorter than in juveniles of *Asterolepis ornata*.

The external submarginal ridge (smr) starts to extend backwards from the spiracular foramen to the posterior end of the SM plate (Figs. 4.2.; 4.4.; 4.16.A). In adults there is no ridge at all (Gross, 1931, Pl. IV, fig. 11). No external ridge has been mentioned in other asterolepids: neither in *Remigolepis* (Stensiö, 1931), nor in *Byssacanthus* (Karatajūte-Talimaa, 1963, p.295).

Small well pronounced spiracular foramen, or the infraspiracular notch (*ispi*, Stensiö 1948, fig.32) or dorsal notch (*dn*, Hemmings, 1978, fig. 5 E-I), is present in approximately foremost third of the submarginal plate (Fig. 4.16. B), like in adults (Gross, 1931, Pl. IV, fig.11). There is a small vertical wall delimiting the spiracular foramen (LDM 260/253). It is also well developed in *Asterolepis scabra* (Nilsson, 1941, p. 52), *Gerdalepis* (Gross, 1941, p.196) and *Stegolepis tuberculata* (Malinovskaya, 1973, p.195).

The dorsal margin (dm) of the plate varies in its configuration with more or less developed semilunar process in its middle part (Fig. 4.16.); it rises backwards from the level of the infraspiracular notch (ispi). The ventral margin (vm) is convex. Postero-dorsal and postero-ventral corners of the plate are well rounded off; the anterior corner (ac) appears rather pointed.

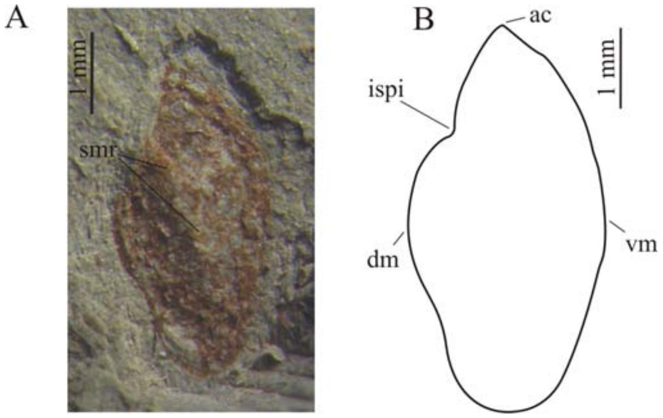


Fig. 4.16. Right submarginal plate (SM) of juvenile of *Asterolepis ornata.* **A,** LDM 260/259a, in dorsal view. **B,** LDM 260/393.

4.16. att. Bruņuzivs *Asterolepis ornata* mazuļa labais žaunu vāks (SM). A, LDM 260/259a, dorsālais skats. B, LDM 260/393.

The SM plate is overlapping by the lateral (La) plate. Areas for the attachment to the La plate are rather weakly pronounced (LDM 260/35, 260/253a): the prespiracular area ($ad_1$) and more less weakly - the postspiracular area ($ad_2$). With the growth the prespiracular area is better developed and is restricted by the narrow and small ridge (LDM 260/78, ontogenetic stage 4). The prespiracular area $ad_1$ is visible even from the external view also (LDM 260/118, ontogenetic stage 3).

The ornamentation of the plate is fine-meshed and reticulate as for the other plates of juveniles, but along the outside margins the distinct ornamentation of several concentric ridges occurred.

### 4.1. 5. Visceral skeleton

The visceral skeleton usually is represented by the pair of suborbital bones, and very seldom by the inferognathal plates (LDM 260/1a), as well as by some other undeterminable small jaw bones (LDM 260/1a). There are also undeterminable fragments of small bones among the material at hand. Part of them has the reticular ornament characteristic of the dermal bones.

**Suborbital** (SO) plate (*mentale* of Nilsson, 1941; Lyarskaya, 1981) often is preserved in upside-down position due to the internal pressure of decomposition gases, and is located near to the place of origin (Figs. 4.17. C; 4.18.; 4.42.; 4.45.). The anterior margin is convex, posterior – straight, lateral – concave (Fig. 4.17. A-C). The shape in general is similar to that in adults (Fig. 4.17. D,E). The shape of the SO plate of the adult individual, figured in Lyarskaya (1981, fig. 73), do not coinside with the materal at hand.

The SO plate clearly exhibits the dorso-lateral process (dlp) and extended ventro-lateral process (vlp), as it is described for *Remigolepis* sp. in Nilsson (1941, Fig. 6 A), although there they are shown conversely (due to upside-down position of the SO plates). The ornament of the plate in juveniles is fine-meshed and reticulate, in adults - stripped. The length of the plate in juveniles comprises 1.25-1.90 mm (appendix 2.10). In adult the only one known detached plate is 25.5 mm long.

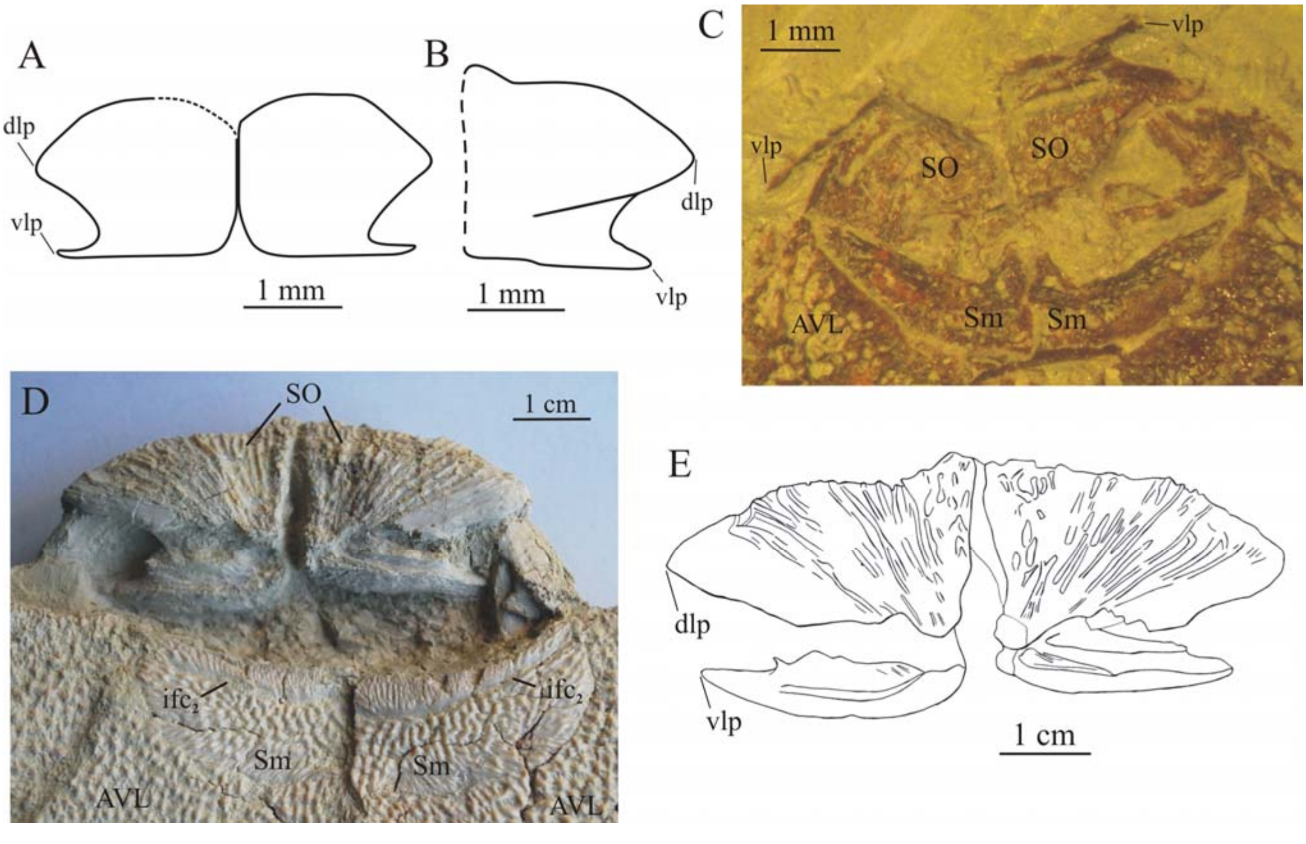


Fig. 4.17.(in previous page) Suborbital (SO) and semilunar (Sm) plates of *Asterolepis ornata*. **A-C**, of juvenile individuals. A, a pair of SO bones, LDM 260/100a. B, right SO, LDM 260/402a, in visceral view. **C**, a pair of SO bones in upside-down position in visceral view; a pair of Sm plates in external view. LDM 260/1. **D,** a pair of SO and Sm bones of adult individual. UP 10/1-1, in external view. **E**, a pair of SO bones of the same individual.

4.17. att. (iepr.lpp.) Bruņuzivs *Asterolepis ornata* zemacu kauls (SO) un pusmēness kauls (Sm). **A-C**, mazuļiem. A, zemacu kaulu pāris (SO), LDM 260/100a. B, labais SO, LDM 260/402a, iekšskats. **C**, zemacu kaulu pāris (SO) in upside-down position, iekšskats; pusmēness kaulu pāris (Sm), ārskats. LDM 260/1. **D,** pieauguša īpatņa SO un Sm kaulu pāri. UP 10/1-1, ārskats. **E**, SO kaulu pāris iepriekšējam īpatnim.

### 4.1.6. Trunk-armour

The dermal armour of juveniles is more angular than in adults (Fig. 4.3.). The trunk armour is strengthened by the system of strongly developed ridges. The dorsal and ventral walls of the trunk armour meet at well-pronounced angles and externally are marked by the dorso-lateral ridge (dlr) and the ventro-lateral ridge (vlr). These ridges encountered the lateral walls of both side of the placoderm fish. Ventral wall extends somewhat further backwards than the other walls.

It is especially characteristic of trunk-armour that, contrary to what is the case in adult *Asterolepis*, it has an independent posterior lateral (PL) and posterior dorsolateral plate (PDL) instead of a single mixilateral (MxL). The smallest individuals reveal an unossified rhombic region on the lateral wall – lateral fontanel (Figs. 4.19.; 4.20), and unossified rhombic area on the ventral wall – ventral fontanel (Fig. 4.4. B).

Disarticulated dermal bones of the trunk-shield are much more common than skull remains, therefore more suitable for investigations. With regard to the sutures of trunk-armour plates they are normally overlapped as in adults.

***Dorsal wall*** is broadest at its anterior margin (in adults - at it's middle). The anterior margin is a little convex (in adults - concave). Laterally it is produced forwards and takes part in the formation of the processus obstans (pro). Posterior margin is convex and presents a well-pronounced posterior angle (pa) of PMD; the margin has no such protruded posterior corner as in adults. The posterior angle is similar to that in adult of *Asterolepis radiata* (Karatajūte-Talimaa, 1963, Pl. 18).

The tergal angle is situated between the anterior third and the anterior fourth of the AMD. The dorsal median ridge (dmr) from the tergal angle extends backwards to the posterior angle (pa) of the wall, forming a well-marked crest on the PMD (Fig. 4.4. A), and dividing the dorsal lamina into right and left halves. Frequently the *dmr* occurs also in some distance in front of the tergal angle. The *dmr* is sharp edged on the whole PMD plate and there it is a little highest than on the AMD plate.

In adults the *dmr* is rounded off and less pronounced: it weakly appeared somewhat in front of the tergal angle (Lyarskaya, 1981, p. 110). As pointed out by Stensiö (1948, p. 104), this ridge is more strongly developed in young individual of *Bothriolepis* (*B.canadensis, B.groenlandica*) than in older ones. The same is seen also for *B.askini* (Young, 1988, fig. 21).

The presence of a paired oblique transverse ridge (otr) is also one of the special characters of immaturity: it's not visible in adult *Asterolepis ornata*. The *otr* ridge runs off in an antero-lateral direction from the tergal angle and is continuing on the each ADL plate reaching the *dlr* ridge. In juveniles of *B.canadensis* it is developed only for some distance nearest to the tergal angle (Stensiö, 1948, figs. 43A, 96-98, 202), but in several cases it is also traceable on the ADL near the processus obstans also (ibid.: fig. 92).

***Ventral wall*** have several peculiarities which distinct it much from that in adults (Figs. 4.3.; 4.4.; 4.18.): 1) the ventral wall is robust and angular; 2) the subcephalic division is proportionally longer; 3) the posterior part of the wall has angular processes formed by the both PVL plates; 4) the uncovered central part of the ventral wall revealed no developed MV plate or reveal the initial ossification of this plate.

The ventral wall in juveniles is widest at the prepectoral region (in adults - at middle of the wall), and is narrowest in the posterior end. The width/length ratio of the ventral wall is about 0.5, being slightly narrower than in adults. The ventral wall is flat.

Subanal part protrudes somewhat behind the projection of the dorsal wall as in adults. Posterior margin is well thickened (as in adults) and is marked by angular posterior processes of the PVL plates (in adults – straight). Central part of the ventral wall of youngest individuals lacks ossified median ventral plate.

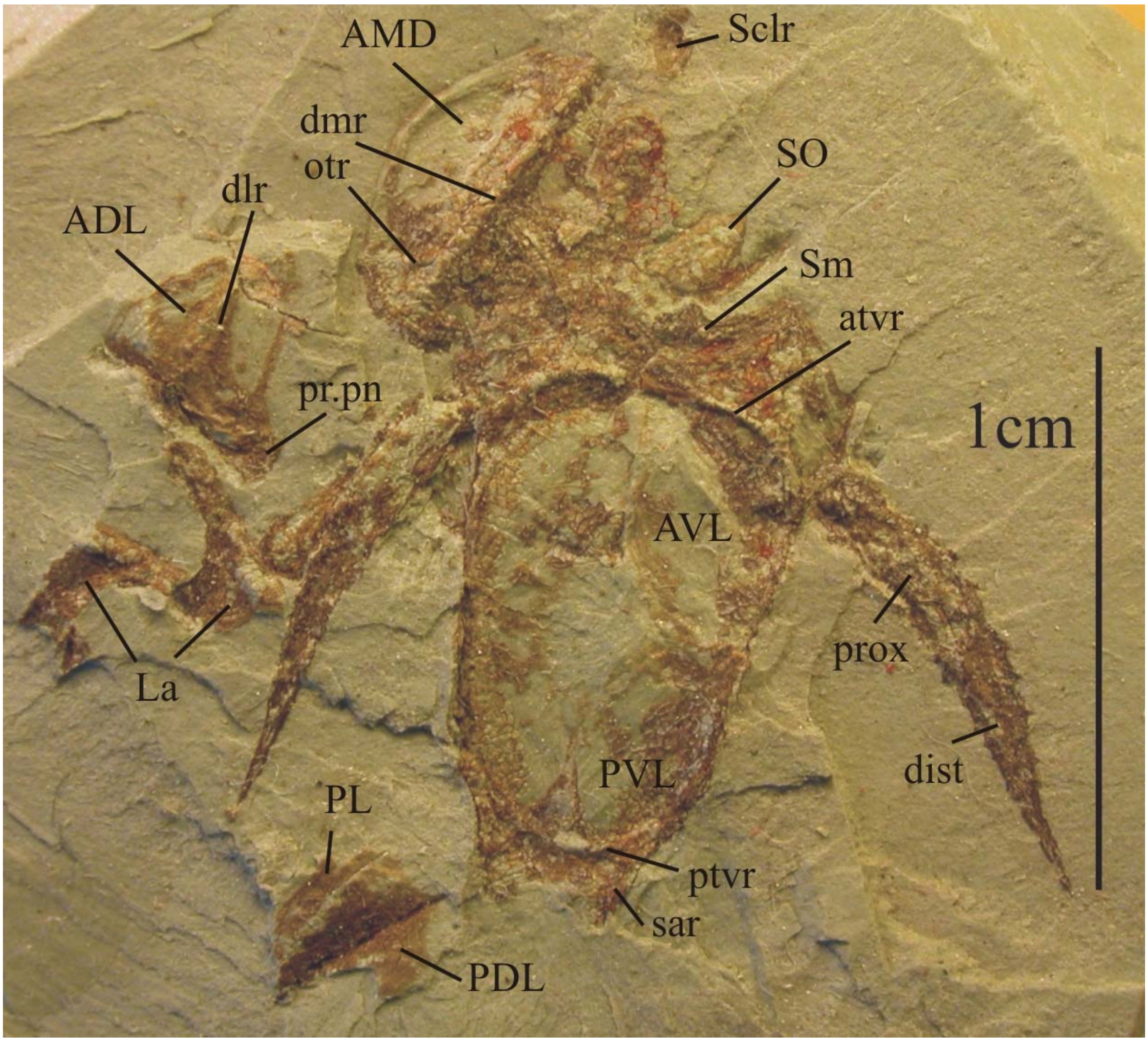


Fig. 4.18. Disarticulated juvenile individual of *Asterolepis ornata* LDM 260/87a. Ventral wall of the trunk with detached armour plates from the dorsal side. This specimen mainly was used for the reconstruction.

4.18. att. Bruņuzivs *Asterolepis ornata* fragmentēts mazulis LDM 260/87a. Ķermeņa ventrālās sienas bruņu plātnes ar atsevišķām muguras un laterālo sieniņu bruņu plātnēm (AMD, ADL, PDL, PL). Pēc šī parauga gk. tika veikta rekonstrukcija.

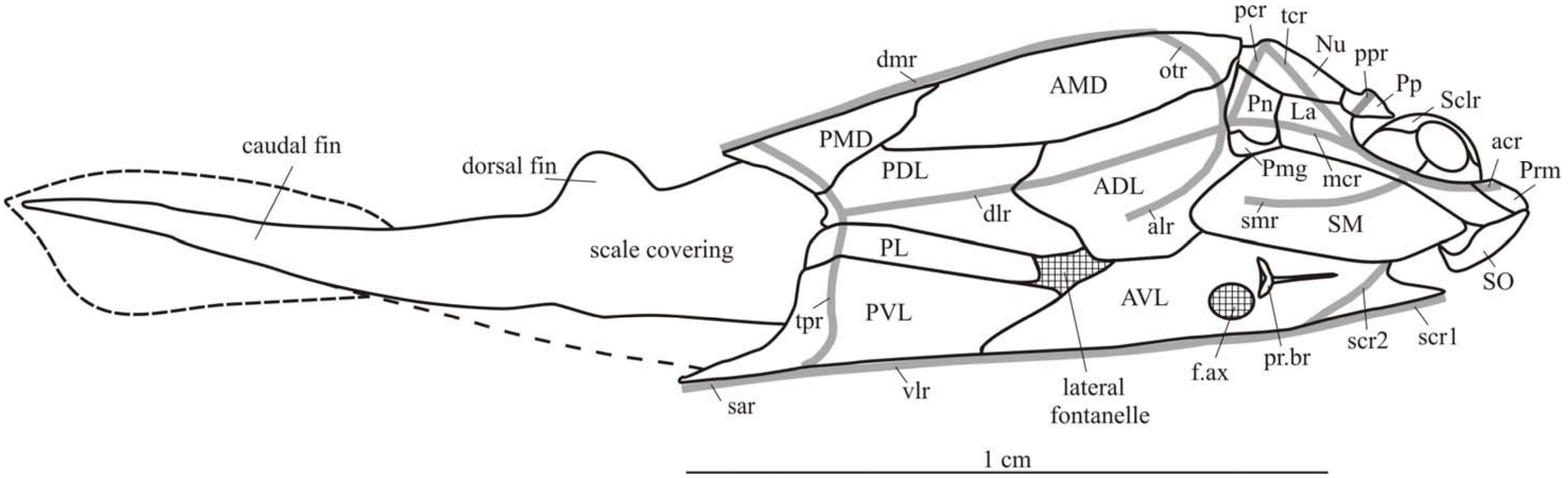


Fig. 4.19. Reconstruction of juvenile of *Asterolepis ornata*, the 2nd stage of ontogeny in lateral view (without pectoral fins). Grey solid lines indicate the ridge system.

4.19. att. Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija, otrā ontoģenētiskās attīstības stadija, sānskats (bez krūšu peldspurām). Pelēkās līnijas iezīmē valnīšu sistēmu.

Anterior margin of the wall is slightly concave with small processes in its central part, formed by the pair of the semilunar plates (Fig. 4.4. B). Anterior lateral margins are markedly thickened. Anterior lateral corners (al) are sharp (in adults - well rounded off), and they are situated on the lateral edge of the subcephalic division (in adults - on the anterior margin). Detailed description of them follows for the AVL plate.

The longitudinal ventro-lateral ridges (vlr) fuse in the anterior and posterior parts of the ventral wall, thus separating the subcephalic and subanal parts from the rest of the wall. In subanal part the paired subanal ridges (sar) stretch to the posterior margin of the wall, forming the anterior transverse ventral ridge (atvr) and posterior transverse ventral ridge (ptvr), respectively. In the subcephalic part of the wall two paired subcephalic ridges occured (scr1, scr2). They are of different length (Fig. 4.4. B); the first one (scr1) is the longest, and it is slightly concave. Dorso-lateral ridges (dlr) and ventro-lateral ridges (vlr) are connected by means of the short transverse posterior ridge (tpr), situated on each PDL plate.

The **crista transversalis interna anterior** (cit) is well developed and most clearly pronounced between lateral and ventral walls, less - between dorsal and lateral walls. Dorsal wall devoid the crista, as in adult *Asterolepis*, and lacks a postlevator thickening. The crest forms a high lamina of bone on the lateral wall. The ventral division of the crest, - the postbranchial crest (cr.pb) decreases in height in a medial direction and is low near the suture between the both AVL plates. It diagonally crosses the anterior third of the AVL plate.

The **crista transversalis interna posterior** (cr.tp) is developed around the whole posterior opening of the trunk-armour, and is more rounded and lower than the *cit*. Dorsally, the *cr.tp* is well developed. It is thickened and rounded off in advanced juveniles.

***Lateral walls*** are encountered longitudinally by the *dlr* and *vlr* ridges, and posteriorly by the *tpr* ridge (Fig. 4.19.). The lateral walls usually are dorso-ventrally compressed and crashed. Little part of specimens is preserved laterally. Lateral walls are the shortest walls. Anterior margin is concave in its ventral part; it is convex in upper part, formed by the processus obstans (pro). Posterior margin is concave throughout its extent. There is no difference in the shape from adults.

The lateral wall in the very early stages of the armour development had possessed the lateral fontanel of a rhombic shape between the ADL, AVL, PL and PVL plates. This area gradually decreased with enlarging of the adjacent armour plates. It is well seen in two specimens (UP 10/2-4 and LDM 260/313) representing the connection area between the ADL and AVL plate (Fig. 4.20.), as well as judging from the shape of the ADL plate in specimens LDM 260/156b and LDM 260/200a. The mentioned feature is not known in other antiarchs; seemingly it is due to no having finds of so early ontogenetic stages.

The slope dorsal margin of the adjacent PVL plate in very small individual of *Bothriolepis askini* (Young, 1988, figs. 15A, 23 F,G) point to the possible presence of the lateral fontanel in juvenile stages of *Bothriolepis* as well.

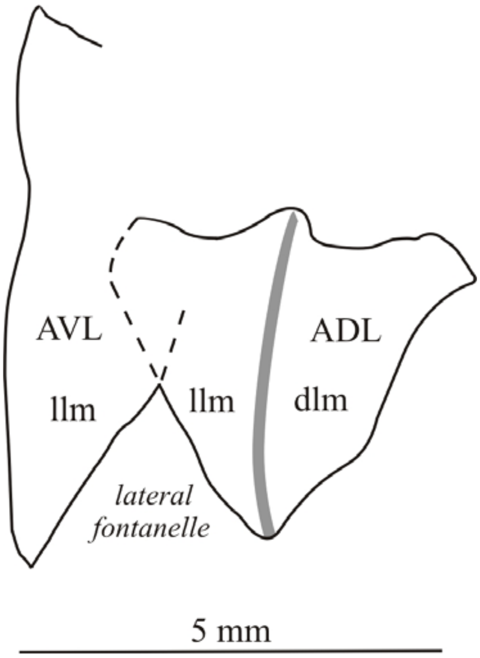


Fig. 4.20. Contact area between the lateral plates ADL and AVL of juvenile of *Asterolepis ornata*, showing lateral fontanel on the lateral wall. Reconstruction of part and a counterpart. UP 10/2-4a,b.

4.20. att. ADL un AVL bruņu plātņu kontaktējošais laukums bruņuzivs *Asterolepis ornata* mazulim, redzams sānu atvērums laterālajā sienā. Rekonstrukcija pēc abām parauga pusēm. UP 10/2-4a,b.

## Trunk armour plates

The shape of the **anterior median dorsal** plate (AMD) in juveniles somewhat differs from that in adults (Fig. 4.3.), although the ratio length/width of the plate do not exhibit changes during the growth (appendix 2.12., ratio a/b). In juveniles the plate is relatively broad, especially in its anterior half (Figs. 4.4.; 4.21. A,B).

The anterior margin of the AMD plate in juveniles varies from straight to a little concave in the shape, exhibiting a median notch (LDM 260/363). Such variable anterior margin is also seen in *Bothriolepis canadensis* (Stensiö, 1948, figs. 121-125). The ratio the width of the plate/width of the anterior margin changes from 2.43 in juveniles up to 9.65 in adults of *Asterolepis ornata* (appendix 2.12: ratio $b/b_1$). In adults the plate is always narrow anteriorly (Figs. 4.3.; 4.21. F). The broad anterior margin is also known in *Pterichthyodes* (Hemmings, 1978, fig. 24), *Gerdalepis* (Gross, 1941, fig. 7), *Lepadolepis* (Gross, 1933, fig. 4) and *Byssacanthus* (Karatajūte-Talimaa, 1960, fig. 2). All in all the AMD in juveniles of *Asterolepis ornata* is broad anteriorly somewhat like as in bothriolepids.

The posterior margin of the plate bears a remarkable posterior median process (pr.p) and is concave on either side of it, forming well-developed postero-lateral corners (pcl). In adults the posterior margin is variable: undulate (Fig 4.21. F), straight or slightly concave (Lyarskaya, 1981, p.110; fig. 78), but no posterior median process (pr.p) is visible._The strongly developed posterior median process in small individuals of *Bothriolepis canadensis* is considered as the character of immaturity (Stensio, 1948, p. 212, fig. 121). The relative size of the process decreases during growth (ibid.: p. 213).

Antero-lateral corner (alc) is rounded off. Behind it, as in *Bothriolepis* (Stensiö, 1948, figs. 43, 44), and *Byssacanthus* (Gross, 1940, fig. 10), some specimens (LDM 260/87) bear a well marked postnuchal notch (npn). The rounded postlevator process (pr.pl) behind it is well pronounced in all juveniles (Fig. 4.21. A-D). Sometimes these two elements are weakly pronounced also in subadult (Fig. 4.21. E) and adult *Asterolepis ornata* (Lyarskaya, 1981, Pl. 27), as well as in *A.syasiensis* (Lyarskaya, 1981, Pl. 35, fig. 1), *A.scabra* (Nilsson, 1941, fig. 10) and in *A.estonica* (Karatajūte-Talimaa, 1963, Pl. 1, fig. 3). The distance between the anterior margin and the tergal angle accounts about one fourth of the total length of the plate, as in adults.

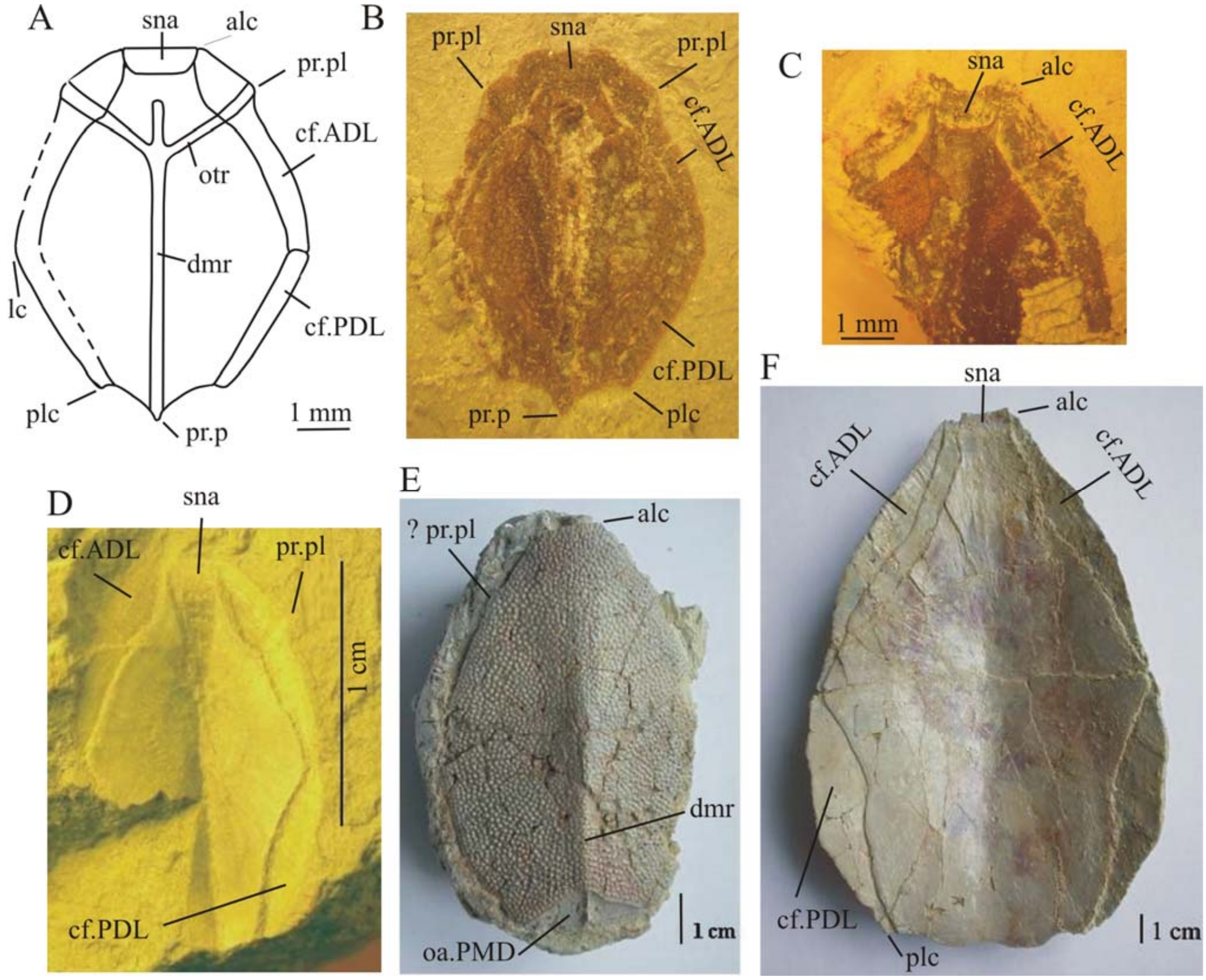


Fig. 4.21. Anterior median dorsal (AMD) plate of *Asterolepis ornata*. **A-D**, of juveniles. A, B, in visceral view. Double lines indicate the grooves corresponding to the dorsal median ridge (dmr) and oblique transverse ridge (otr). LDM 260/248. C, in visceral view, LDM 260/363. D, in visceral view, advanced juvenile in about 5th stage of ontogeny, LDM 260/351. **E**, of subadult, in dorsal view. UP 10/1-7. **F**, of adult, in visceral view. UP 10/1-3.

4.21. att. Bruņuzivs *Asterolepis ornata* priekšējā vidējā muguras plātne (AMD). **A-D**, mazuļiem. A, B, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsālimediālam valnītim (dmr) un slīpam šķērseniskam valnītim (otr) dorsālajā pusē. LDM 260/248. C, iekšskats, LDM 260/363. D, piektā ontoģenētiskās attīstības stadija, iekšskats, LDM 260/351. **E**, pusaugu īpatnis, dorsālais skats. UP 10/1-7. **F**, pieaudzis īpatnis, iekšskats. UP 10/1-3.

Lateral corner of the plate (lc) is well marked only in few specimens. It situates somewhat behind the middle of the lateral margin. A small notch sometimes appears on the border of overlapped areas for the ADL and PDL plate (Fig. 4.21. A). In adults the lateral corners either are sharp or rounded off (Lyarskaya, 1981, figs. 78,79).

The overlapping areas for ADL and PDL in juveniles don't narrowed at the lateral corners as it is seen in subadults and adults (Fig. 21.A,E,F). The shape of the overlapping area of ADL plate in juveniles is distinct from that in the adult *Asterolepis,* and is somewhat similar to that in *Bothriolepis canadensis* (Stensiö, 1948, fig. 126). It is broad in its' anterior part and corresponds to the shape of the dorso-medial process of the ADL plate.

The length of the AMD plate in studied specimens comprises 4.50-13.80 mm in juveniles, 24.0-69.5 mm in subadults, 106.0-182.0 mm in adults. The longest detached AMD plate of juvenile (Fig. 4.21. D) morphologically already resembles that in adult: 1) the above mentioned overlapped areas narrow as in adults; 2) the anterior margin narrow as in adults.

The plate bears the remarkable dorso-median ridge (dmr) and two oblique transverse ridges (otr). The latter forms the postlevator process in juveniles and subadult (pr.pl) (Fig. 4.21.A,B,D,E) and continue on the ADL plate (Fig. 4.4.). The oblique transverse ridge is not preserved in adults of *Asterolepis ornata* (therefore the postlevator process is absent also), but is known in the small individuals of other antiarchs: bothriolepids: *Bothriolepis canadensis* (Stensiö, 1948, p.118, fig. 43. A) and *Bothriolepis askini* (Young, 1988, fig. 23. A). The *otr* in small individuals of *Bothriolepis canadensis* is indicated as one of the characters of immaturity (Stensio, 1948, p. 213).

The supranuchal area (sna) became gradually marked during the growth of the individuals (Fig. 4.21. A-D). The same is pointed out for juveniles of *Bothriolepis canadensis* (Stensiö, 1948, p.281). Minute ridges restrict the supranuchal area of *Asterolepis* juveniles laterally (Fig. 4.21. A). In adults this area is well marked (Gross, 1931, Pl. VII, fig. 11).

The internal face of the plate is smooth. The grooves from the corresponding external ridges (otr and dmr) are remarkable throughout their extent. Underneath the *dmr* is a longitudinally rough area.

The **posterior median dorsal** plate (PMD) is broadest across the lateral corners (lc), in adults – in the distance between the lateral corners and the postero-lateral corners (plc) (Fig. 4.22.). The length/breadth ratio of the PMD plate does not exhibit significant changes during the growth of the fish.

The anterior margin of the plate is produced into an anterior corner (ac). It becomes less pronounced in advanced juveniles and adults (Fig. 4.22. A,C). The posterior margin has more or less marked convexity and is produced into a well-pronounced posterior corner (pc). In some specimens (LDM 260/259, 260/528) this corner forms a distinct tapered process. The posterior margin of adults is convex also (Lyarskaya, 1981, fig. 81), the posterior corner appears angular shaped. The oldest adults exhibit well-marked posterior notch (pn, Fig. 4.22. C,D).

Anterior part of the lateral margin is convex; further backwards it is rather straight or with a slight concavity in front of the well-marked lateral corners (lc). Antero-lateral corner (alc) is remarkable in youngest juveniles and not pronounced in advanced ones. Its` presence (Fig. 4.22.D) or absence seems to be a variable feature in adults also (Lyarskaya, 1981, fig. 81). The postero-lateral corner (plc) in juveniles is angular or rounded off, and angular in adults.

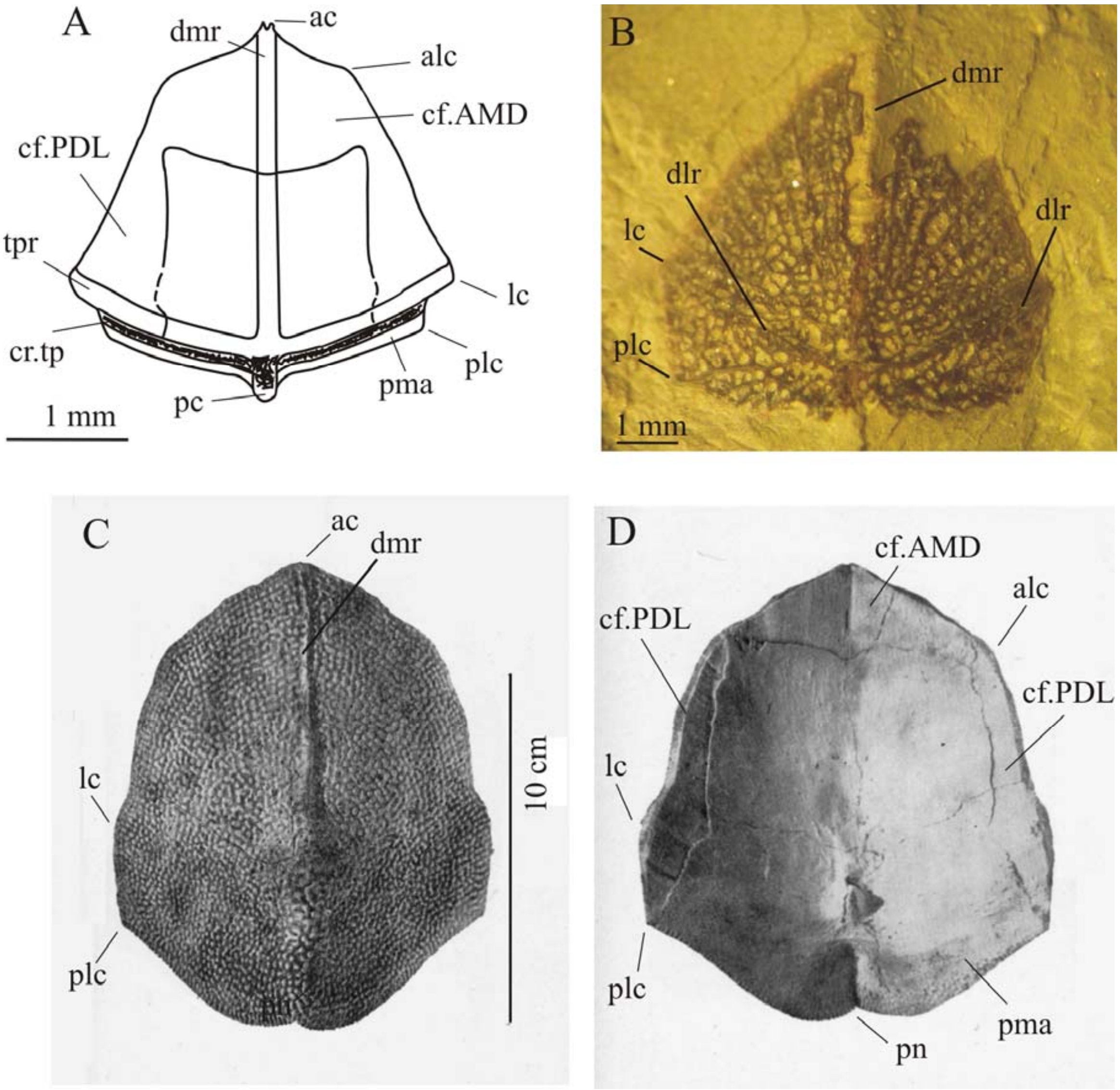


Fig. 4.22. Posterior median dorsal plate (PMD) of *Asterolepis ornata*. **A, B,** of juvenile. Lode quarry, Lode Fm. A, in visceral view. Double lines indicate the grooves corresponding to the dorsal median ridge (dmr) and to dorsal lateral ridge (dlr). LDM 260/526. B, of advanced juvenile, the 4th ontogenetic stage, LDM 260/529, in dorsal view. **C, D,** of adult. Sigulda town, Gauja Fm. C, (Karatajūte-Talimaa, 1963, Pl. VI, Fig. 3). D, (Karatajūte-Talimaa, 1963, Pl. VII, Fig. 1).VII, Fig. 1).

4.22. att. Bruņuzivs *Asterolepis ornata* pakaļējā muguras plātne (PMD). **A, B,** mazuļiem. A, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-mediālam valnītim (dmr) un dorsāli-laterālajam valnītim (dlr). LDM 260/526. B, Ceturtā ontoģenētiskās attīstības stadija, LDM 260/529, dorsālais skats. **C, D,** pieaugušam īpatnim. Sigulda, Gaujas svīta. C, (Karatajūte-Talimaa, 1963, Pl. VI, Fig. 3). D, (Karatajūte-Talimaa, 1963, Pl. VII, Fig. 1).

The crista transversalis interna posterior (cr.tp) lies in some distance of the posterior margin of the PMD plate, where the posterior marginal area (pma) is broad and varies in length (Fig. 4.22. A). The lateral parts of the crest are pronounced, but the ventral part rapidly decreases in height.

The plate bears a well-pronounced *dmr* ridge. In adults it is marked only in the posterior part of the plate, but as well is clearly pronounced in some other asterolepids: *Asterolepis dellei* (Gross, 1940, pl.3, fig.8), *Asterolepis radiata* (Karatajūte-Talimaa, 1963, figs. 46.-2, 48.) and *Asterolepis* sp. 3 (ibid.: fig. 21). The posterior margin bears the *tpr* ridge. These two ridges formed the remarkable ridge crest with ends in a protruding posterior corner (pc) of the plate (Figs. 4.4. A; 4.22. A).

The length of the PMD plate in studied specimens comprises 2.40-5.60 mm in juveniles 20.1-40.5 mm, in subadults, and 74.9-127.0 mm in adults. The ratio length of the anterior part of the plate/posterior part changes from 1.25-1.43 in juveniles up to 2.21-3.62 in subadults and adults (appendix 2.13., ratio $a_1/a_2$).

The **anterior dorso-lateral** plate (ADL) is well preserved in numerous detached specimens, but is crashed in articulated and dorso-ventrally flattened ones. The shape of the ADL of juveniles is considerably different from that in adults: the change occurred in both dorsal and lateral lamina (Fig. 4.23. A-E), separated by the dorsolateral ridge (dlr). The dorsal lamina (dlm) is broadest and the lateral lamina (llm) is highest across the foremost part of the plate. In adult *Asterolepis ornata* the maximal width and height of the corresponding laminae is across the anterior and the middle parts of the plate, respectively (Fig. 4.23. F). The width of the dorsal lamina relatively increases during the growth of the fish: the ratio changes from 1.56 in juveniles up to 2.96 in adults (appendix 2.14., ratio $a_1/b$). The length of the ADL plate (without processus obstans) in studied juveniles comprises 2.80-7.70 mm, 17.5 mm in only available subadult, 53.0-126.5 mm in adults.

The dorsal margin of the plate is convex anteriorly, where it forms a remarkable angular internal postlevator process (pr.pn), but generally somewhat concave further backwards. The exception is for the very early stage of the development (Fig. 4.23.A), which exhibit a very narrow dorsal lamina directly behind the postlevator process and a convex dorsal margin further backwards. The shape of the mentioned process gradually changes during the growth: from extended to angular and protruded in juveniles, and pointed in adults (Figs. 4.18.; 4.23.). It exhibits a transverse ridge on the visceral side. The postlevator process (pr.pn) is overlapped by the the AMD plate (Fig. 4.23. B,D-F).

The posterior margin of the plate is produced into a remarkable and tapered posterior corner (pc) at the dorso-lateral ridge (dlr). The posterior-lateral corner (plc) is clearly distinguishable, although seldom appeared as well rounded off. The shape of the ventral margin changes during the growth: in very young individuals it is straight, then became slightly undulating or convex in more advanced juveniles (Fig. 4.23. C, D), as in adults (ibid.: F). The anterior margin is strongly convex on the processus obstans (pro) and a little concave dorso-medially to that process.

Processus obstans (pro), as in adults, is broad and consists from a ventral and a medial part (Gross, 1933 b, fig. 3A; Karatajūte-Talimaa, 1963, fig. 34). In juveniles the more protruded is the ventral part, not medial, as it is seen in adults. In the specimen LDM 260/419 the ventral part of the processus obstans exhibit a narrow belt that obviously represents the overlapping area for the postmarginal plate (Pmg) as it is seen in adults. The overlapping areas with the distalmost parts of the adjacent the AMD and AVL plates are very wide and long (Fig. 4.23. B,D), for the PDL plate – rather long (the length of the overlapping area for the PDL comprises up to 1/4 of the length of the ADL plate).

The articular fossa (f.art) presumably is present in specimen LDM 260/414. It is small and weakly pronounced. It stretches in a short distance along the anterior margin from the processus obstans and is bounded below by a weakly developed infra-articular crista (cri).

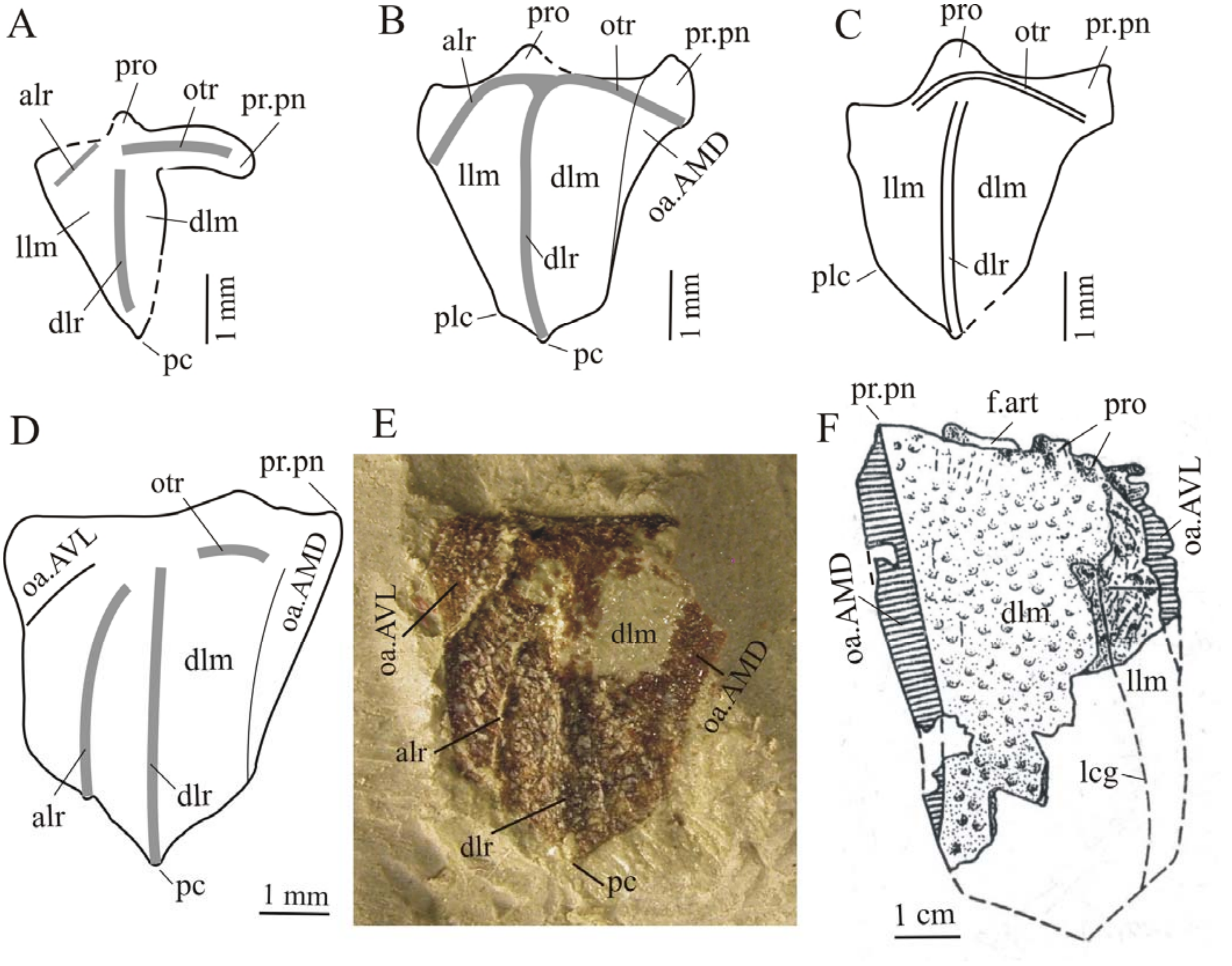


Fig. 4.23. Sequence of developmental stages of the anterior dorso-lateral plate (ADL) of *Asterolepis ornata*. **A-E**, left ADL of juvenile. Lode quarry, Lode Fm. A, the 1st stage of ontogeny, LDM 260/200, in dorsal view. B, the 2nd stage of ontogeny, LDM 260/410, in dorsal view. C, the 2nd stage of ontogeny, Double lines indicate the grooves corresponding to the dorsal lateral ridge (dlr) and oblique transverse ridge (otr). LDM 260/87a,b, in visceral view. D, E, the 3rd stage of ontogeny, LDM 260/252a, in external view (D-drawn from a part and a counterpart). **F**, right ADL of adult, (Karatajūte-Talimaa, 1963, Fig. 34), in dorsal view. Ķūķu Cliff, Gauja Fm.

4.23. att. Secīga attīstība priekšējai muguras-sānu plātnei (ADL) bruņuzivīm *Asterolepis ornata*. **A-E**, kreisā ADL mazuļiem. A, Pirmā ontoģenētiskās attīstības stadija. LDM 260/200, dorsālais skats. B, Otrā ontoģenētiskās attīstības stadija, LDM 260/410, dorsālais skats. C, Otrā ontoģenētiskās attīstības stadija. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-laterālajam valnītim (dlr) un slīpam šķērseniskam valnītim (otr). LDM 260/87a,b, iekšskats. D, E, Trešā ontoģenētiskās attīstības stadija, LDM 260/252a, ārskats (D, zīmēts no abām parauga pusītēm). **F**, labā ADL no pieauguša indivīda, (Karatajūte-Talimaa, 1963, Fig. 34), dorsālais skats. Ķūķu iezis, Gaujas svīta.

The connection between the ADL and AVL plates exhibits the lateral fontanel on the lateral wall of juvenile individuals (Figs. 4.19.; 4.20.). The shape of the fontanel must have been rhomboid and rather large: it is similar in size for the MV plate in the ventral wall, as it can be judged from the ADL and AVL connection. The dense connective tissue might have covered it. The fontanel became overgrown by the adjacent four plates (ADL, AVL, PDL, PVL) during the growth of the individual. Such lateral fontanel has not been previously described in antiarchs, as mentioned before.

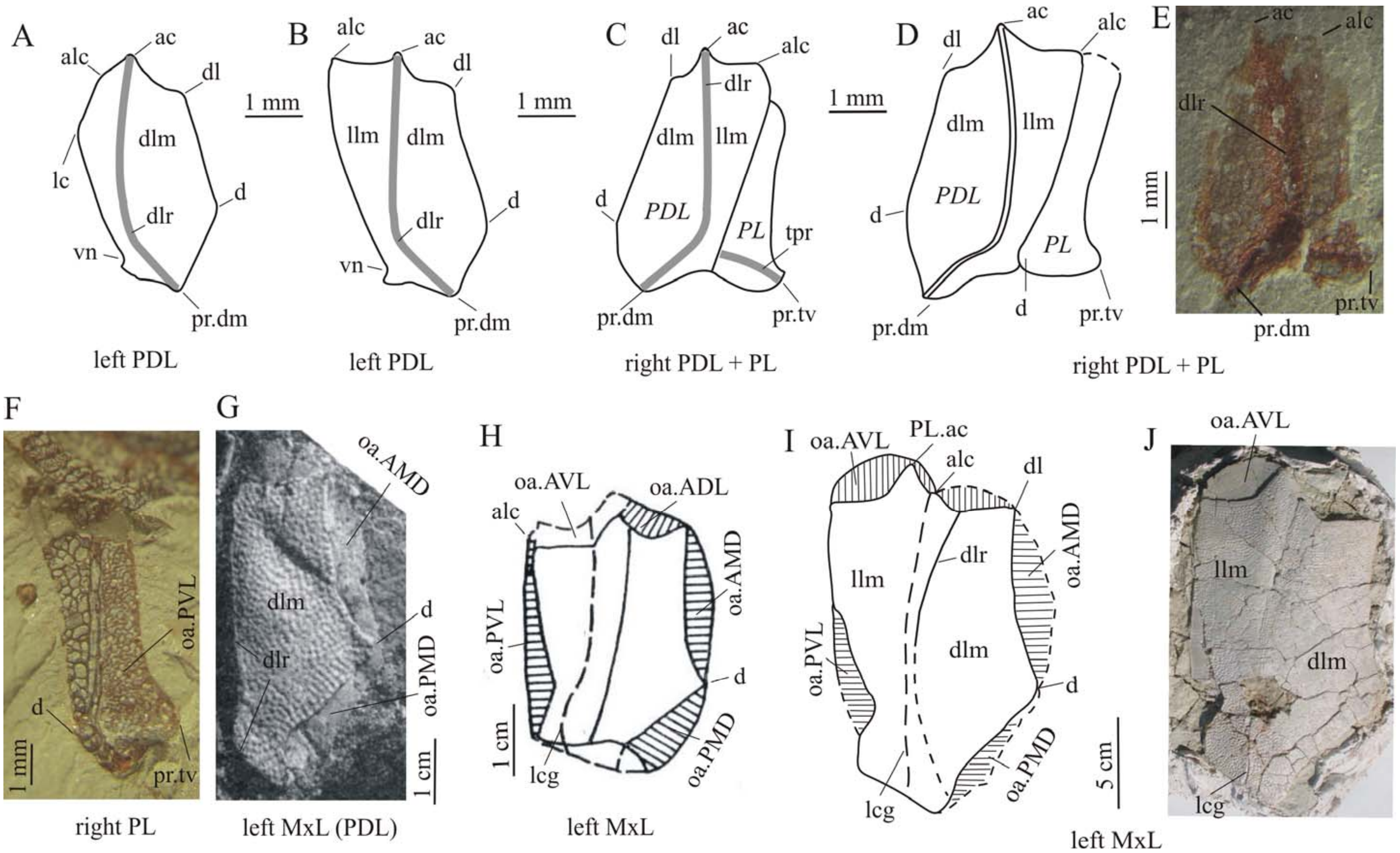
The lateral lamina of the ADL plate in juveniles bears a diagonally located anterior lateral ridge (alr), which stretches backwards. In advanced juveniles this ridge reaches the posterior margin of the plate (Fig. 4.23. D,E) and might have been stretched also on the PDL plate. Such ridge is seen on the small ADL plate of *Asterolepis ornata* illustrated by Gross (1931, Pl. VII, fig. 4). Supposedly, this ADL is from the subadult individual comparable with the largest advanced juvenile (ontogenetic stage 5, described in the chapter 4.2.3.). This ridge (alr) is not seen in adults of *Asterolepis*, as well as in the related antiarchs. Nevertheless it is rather well developed in non-related antiarchs, - for example, studies in the Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, show that it is rather prominent in the small-sized specimens of Chinese antiarchs *Yunnanolepis porifera, Chuchinolepis gracilis,* and *Minicrania lirouyii*. The mentioned small ridge is not seen in figures by Zhu (1996, Figs. 7A, 20.A), but is well seen in photo in Zhu, Janvier (1996, Fig. 2).

The oblique transverse ridge (otr) from the adjacent AMD plate continues to the direction of the processus obstans (pro) of the ADL plate and there joins to the dorsolateral ridge (dlr) and the anterior lateral ridge (alr) of the same plate.

The **posterior dorso-lateral** plate (PDL) is a separate plate and not fused with the posterior lateral (PL) plate in the trunk-armour of juveniles (Figs. 4.19.; 4.24. A-F). In subadults and adults they had been fused (Fig. 4.24. G-J), forming the single mixilateral plate (MxL). The juvenile individuals bear entirely independent two plates: PDL and PL, similarly to that observed in adults of other asterolepids: in *Remigolepis* (Stensiö, 1931, fig. 81), *Pambulaspis* (Young, 1983, fig.7.A), *Byssacanthus* (Karatajūte-Talimaa, 1960, p.296).

The PDL plate is divided into dorsal (dlm) and lateral lamina (llm) by the dorsolateral ridge (dlr). The anterior margin of the plate is somewhat convex in the earliest growth stage (Fig. 4.24. A), later during the growth it changes to almost straight with a pointed anterior corner (ac) at the dorso-lateral ridge (*ibid*.: B-E). The posterior margin is slightly concave. This margin dorsally is directed into a medial dorsal process (pr.dm) at the dorso-lateral ridge and is covered by the lateral corner (lc) of the PMD plate (Fig. 4.22. A); ventrally it forms a small process near the ventral notch (vn). The dorsolateral ridge (dlr) extends from the anterior to posterior margin of the plate. In adult of *Asterolepis ornata* this ridge is weakly developed and disappears in some distance in front of the posterior margin (Fig. 4.24. I).

The dorsal margin of the PDL plate in juveniles has more or less pronounced dorsal corner (d). In front of it the dorsal margin is straight and slopes forwards till the dorso-lateral corner (dl); caudally from the dorsal corner the dorsal margin is rather straight or slightly concave and slopes backwards till the medial dorsal process (pr.dm). In adults the dorsal margin in both directions from the dorsal corner (d) is strongly concave bearing wide overlapped areas of the adjacent AMD and PMD plates. The PDL plate is always broadest across the dorsal corner as in adults. In subadults and adults the dorsal corner is seen only on the visceral surface – between the meeting point of areas overlapped by the AMD and PMD plates (Fig. 4.24. G-I). No overlapped areas are developed on the PDL plate for the adjacent plates in juveniles.



left PDL left PDL right PDL + PL right PDL + PL

right PL left MxL (PDL) left MxL left MxL

Fig. 4.24. **A-F**. Sequence of developmental stages of the posterior dorso-lateral plate (PDL) and posterior lateral plate (PL) of juvenile *Asterolepis ornata*. Lode quarry, Lode Fm. A, left PDL, LDM 260/437ab, in dorsal view; B, left PDL, LDM 260/440ab, in dorsal view. C, right PDL plus PL, LDM 260/87ab, in dorsal view. D, E right PDL plus PL, LDM 260/241ab, in visceral view. Double lines indicate the grooves corresponding to dorsolateral ridge (dlr). F, right PL, LDM 260/152a, in dorsal view. **G**, **H**, left MxL plate of small individual of *Asterolepis ornata*, in dorsal view. Ķūķi Cliff, Gauja Fm. G, after Karatajūte-Talimaa (1963, Pl. V, Fig. 3). H, after Lyarskaya (1981, Fig. 84-2), in dorsal view. **I, J**, left MxL plate of adult individual, UP 10/1-4, in dorsal view. Lode pit, Lode Fm.

4.24. att. (iepr.lpp.) A-F. Secīga attīstība pakaļējai muguras-sānu plātnei (PDL) un pakaļējai-sānu plātnei (PL) bruņuzivju *Asterolepis ornata* mazuļiem. A, kreisā PDL, LDM 260/437ab, dorsālais skats; B, kreisā PDL, LDM 260/440ab, dorsālais skats. C, labā PDL plus PL, LDM 260/87ab, dorsālais skats. D, E labā PDL plus PL, LDM 260/241ab, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-laterālajam valnītim (dlr). F, right PL, LDM 260/152a, dorsālais skats. **G**, **H**, kreisā MxL plātne no neliela *Asterolepis ornata* īpatņa, dorsālais skats. Ķūķu iezis, Gaujas svīta. G, pēc Karatajūte-Talimaa (1963, Pl. V, Fig. 3). H, pēc Lyarskaya (1981, Fig. 84-2), dorsālais skats. **I, J**, kreisā MxL plātne no pieauguša īpatņa, UP 10/1-4, dorsālais skats. Lodes karjers, Lodes svīta.

The lateral lamina (llm) exhibits slight changes of shape during the growth. The ventral margin is slightly convex only in the youngest juveniles (Fig. 4.24. A, B) bearing prominent lateral corner (lc) marking contact with the lateral fontanel (Figs. 4.19.; 4.20.). The lateral corner disappears with the growth of the juvenile due to the overgrowing of the lateral fontanel. The ventral margin during the growth becomes fairly straight in its anterior part, and the *alc* already has been directed ventrally (Fig. 4.24. B-E) as in subadults and adults (Fig. 4.24. H-J). Posteriorly the ventral margin has a distinct ventral notch (vn) for the dorsal corner of the PL plate (Fig. 4.24. F) as in *Remigolepis* (Stensiö, 1931, fig. 85) and *Pambulaspis* (Young, 1983, fig. 7.A). The contact face for the PL plate is correspondingly developed.

The shape of the PDL+PL as a whole in juveniles resembles that of MxL of adult *Asterolepis ornata.* There are differences in following: 1) The anterior corner (ac) in juveniles is located on the protruded part of the dlr ridge (Fig. 4.24. A-E). In adults the dlr ridge on the PDL part of the MxL plate anteriorly ends in a small depression and the protruded corner of the MxL plate is located on the PL part of the plate (PL.ac). 2) The PDL plate in juveniles is longer than the PL plate, in adults it is contrary: the PL part of the MxL plate is the longest one. 3) The posterior margin of the PDL+PL in juveniles is relatively much longer than that of the MxL plate in adults.

The main lateral sensory line groove (lcg) and the bone suture are coincident in adults of *Asterolepis ornata* (Fig. 4.24. I). The same is marked (Young, 1983, p. 77) also for some antiarchs with the independent PDL and PL or showing incipient fusion of PDL and PL plates to form a MxL plate (*Gerdalepis, Stegolepis, Pambulaspis, Sherbonaspis).* The presence of separate PDL and PL plates instead of a single MxL is one of the special characters of immaturity in *Asterolepis ornata*. The length of the PDL plate in studied juveniles comprises 4.15-6.00 mm. The length of the MxL plate in only known subadult is 40.6 mm (Fig. 4.24.H), in adults varies from 118.2 to 163.0 mm (appendix 2.15.).

The **posterior lateral** plate (PL). The dorsal margin is slightly concave in its much longer anterior part, then rising in to a dorsal corner (d) in its posterior part, which fits into the ventral notch (vn) of the ventral margin of the PDL plate (Fig. 4.24. A,B). The ventral margin is concave, but has a slightly downward produced postero-ventral process (pr.tv) near its posterior end. In front of it the margin is slightly deep in a dorso-ventral direction (Fig. 4.24. C,D). The anterior and posterior margins are convex.

The posterior margin is a little longer than anterior one, and is always concave. In advanced juveniles (Figs. 4.24. F; 4.27. E) a distinct concavity is seen in the middle of the posterior margin. This part of the margin together with the postero-ventral process (pr.tv) forms a broad area overlapped by the PVL plate. In adults the corresponding margin in the MxL plate does not exhibit any overlapped area. The other overlapped areas are corresponding to these in adults. The ornamentation of the plate is reticular with smaller and delicate reticulation on the area overlapped by the PVL plate (Figs. 4.24. F; 4.27. E). The length of the PL plate in juveniles comprises 3.60-6.60 mm (appendix 2.15.).

The **anterior ventro-lateral** plate (AVL) is mostly represented by its ventral lamina, whereas its lateral lamina is usually slightly compressed or crashed. The proportions and shape of the plate considerably changes during the growth of fish (Figs. 4.3.; 4.4. B; 4.25.; 4.26. A-D), although the length/width ratio of it does not exhibit remarkable changes during the growth (appendix 2.19., ratio: a/b). The length of the plate in juveniles comprises 5.50-11.40 mm, in adults 78.0-148.0 mm.

The ventral lamina of the AVL plate (Figs. 4.25. A,B,D; 4.26. A) is broadest along the anterior transverse ventral ridge (atvr), and across the middle of the lamina in adults (Fig. 4.26.C). It is from two and a half to three times as long as broad.

The ventral lamina shows notable changes of the mesial margin during the growth (Figs. 4.25. A,B,D; 4.26. A). In the smallest detached AVL plate (Fig. 4.25. A,B) the mesial margin is very strongly concave, showing that the most part of the ventral wall of the fish was occupied by the ventral fontanel. During the growth this margin becomes slightly sinuous in LDM 260/474, 260/483, and convex in LDM 260/461, 260/463, 260/481. The mesial margin in advanced juveniles (Figs. 4.25. D; 4.26. A) exhibit two developed corners ($c_4$ and $c_5$) for contact with the adjacent MV plate ($m_3$). In adults only the corner $c_4$ is well pronounced (Fig. 4.26. C).

The right AVL overlaps the left, so that the ventral lamina of the former is broader than that of the latter. The overlap area of the left AVL has a prominently developed corner $c_2$. It bears a continuation of the *crista transversalis interna anterior* (cit) on an internal overlap area (Fig. 4.25. D), which is complemented by a groove on the external overlap area of the AVL plate.

The lateral lamina of the AVL plate in juveniles (Figs. 4.25. A,B; 4.26. B) is highest across the foramen axillaris (f.ax), whereas in adults it is highest in its posterior part (Fig. 4.26.D). It is nearly four times as long as high in juveniles, seven times in adults (Lyarskaya, 1981, p. 117).

The anterior margin is deeply concave for the semilunar plate (Fig. 4.4.B). The strong allometry appears during growth in the subcephalic division of the ventral lamina. The anterior margin of the plate bears a distinct process, the anterior lateral corner (al, Fig. 4.26. A). A second shorter process, the antero-mesial corner (am) is located mesial to that. In adults all corners on the anterior margin are well rounded off (Fig. 4.26. C), and more protruded is the *al* corner contrary to that in juveniles. Due to that the contact margin with semilunar plate ($m_l$) is relatively shorter in adults. The marked antero-lateral corner (al) shown by Lyarskaya (1981, Fig. 86-2) in fact is an antero-mesial corner (am) and therefore must be referred to the next lateral one as it is seen in a related antiarch *Bothriolepis* (Stensiö, 1948, Figs. 164-166; Young, 1988, Figs. 23. D,E). An additional small process appears between the *al* and the *am* in the smallest individual of *Asterolepis* juveniles (LDM 260/200). This is one of the juvenile features of *Asterolepis*. The sharp *al* corner is seen in adult of *Bothriolepis* (Fig. 4.26. E) and *Sherbonaspis hillsi* (c.l, Young, Gourter, 1981, fig. 18 C), less in *Remigolepis* (Fig. 4.26. G).

The region around the *al* corner in adult *Asterolepis* (Fig. 4.26. C), as well as in bothriolepids (Stensiö, 1948, fig. 166. D) considerably protrudes forward. In juveniles the more protruded region is around the antero-mesial corner (am) corner (Fig. 4.26. A).

The dorsal margin of the lateral lamina exhibits convexity backwards the *al* corners and is slightly concave in its posterior part. The lamina usually is deformed and due to that the antero-dorsal corner (adc) of the lateral lamina rarely is well preserved (Fig. 4.26. B). The posterior part of the lateral lamina is low as in adult of *Bothriolepis* (Fig. 4.26. F), in contrary to that in adult of *Asterolepis* (Fig. 4.26. D). This is one more juvenile feature, which could have been appeared in adults of the other antiarchs.

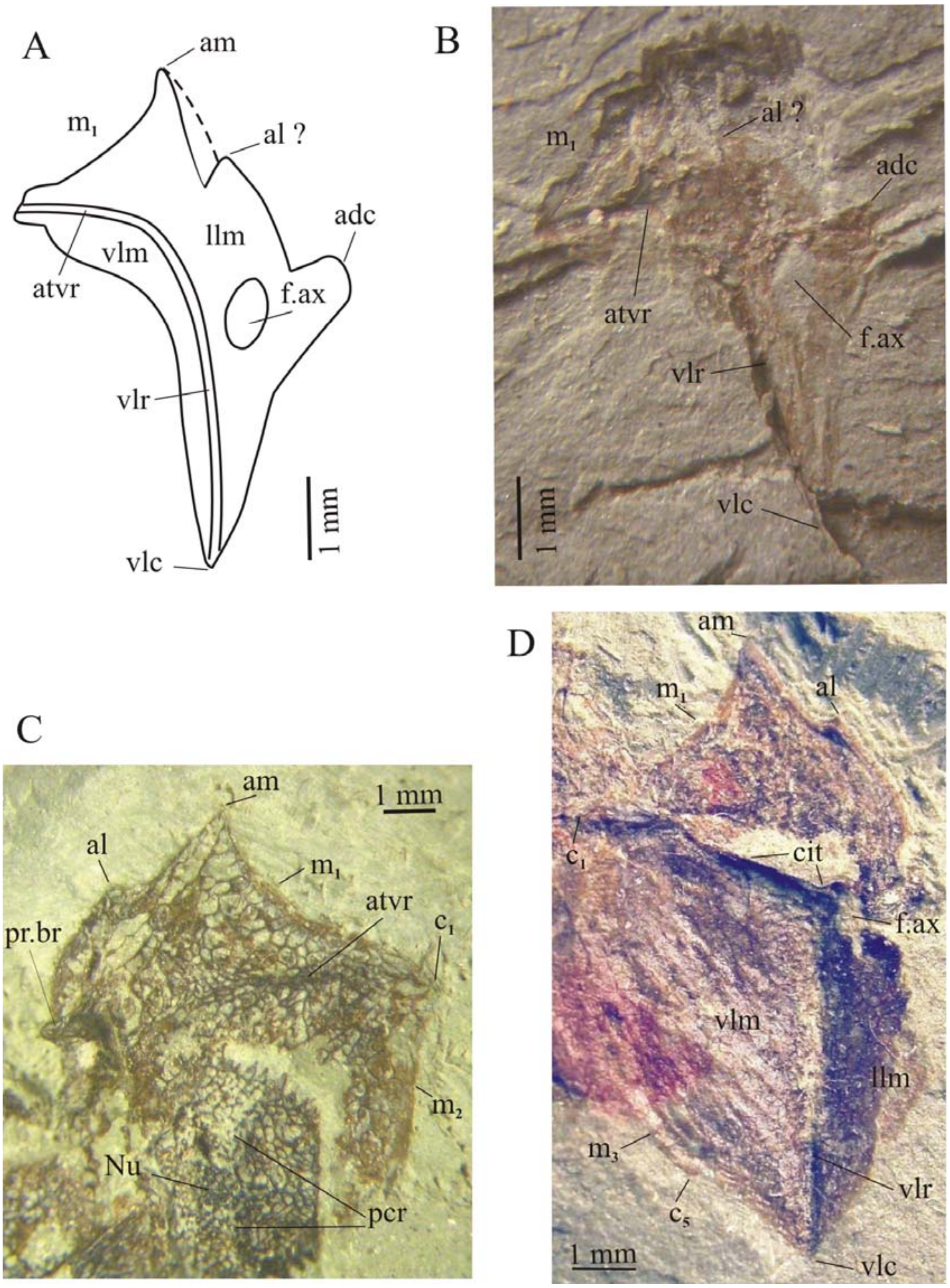


Fig. 4.25. The right anterior ventro-lateral plate (AVL) of juvenile of *Asterolepis ornata*. **A, B,** the 1st stage of ontogeny. LDM 260/458, in visceral view. Double lines indicate the grooves corresponding to the ventro lateral ridge (vlr) and the anterior transverse ventral ridge (atvr). **C, D,** the 2nd stage of ontogeny. C, LDM 260/250a, in external view. D, LDM 260/248b, in visceral view.

4.25. att. Bruņuzivs *Asterolepis ornata* mazuļa priekšējā vēdera-sānu plātne (AVL). A, B, Pirmā ontoģenētiskās attīstības stadija. LDM 260/458, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst ventrāli-laterālajam un AVL plātnes priekšējam šķērseniskajam vēdera valnītim (atvr). C, D, Otrā ontoģenētiskās attīstības stadija. C, LDM 260/250a, ārskats. D, LDM 260/248b, iekšskats.

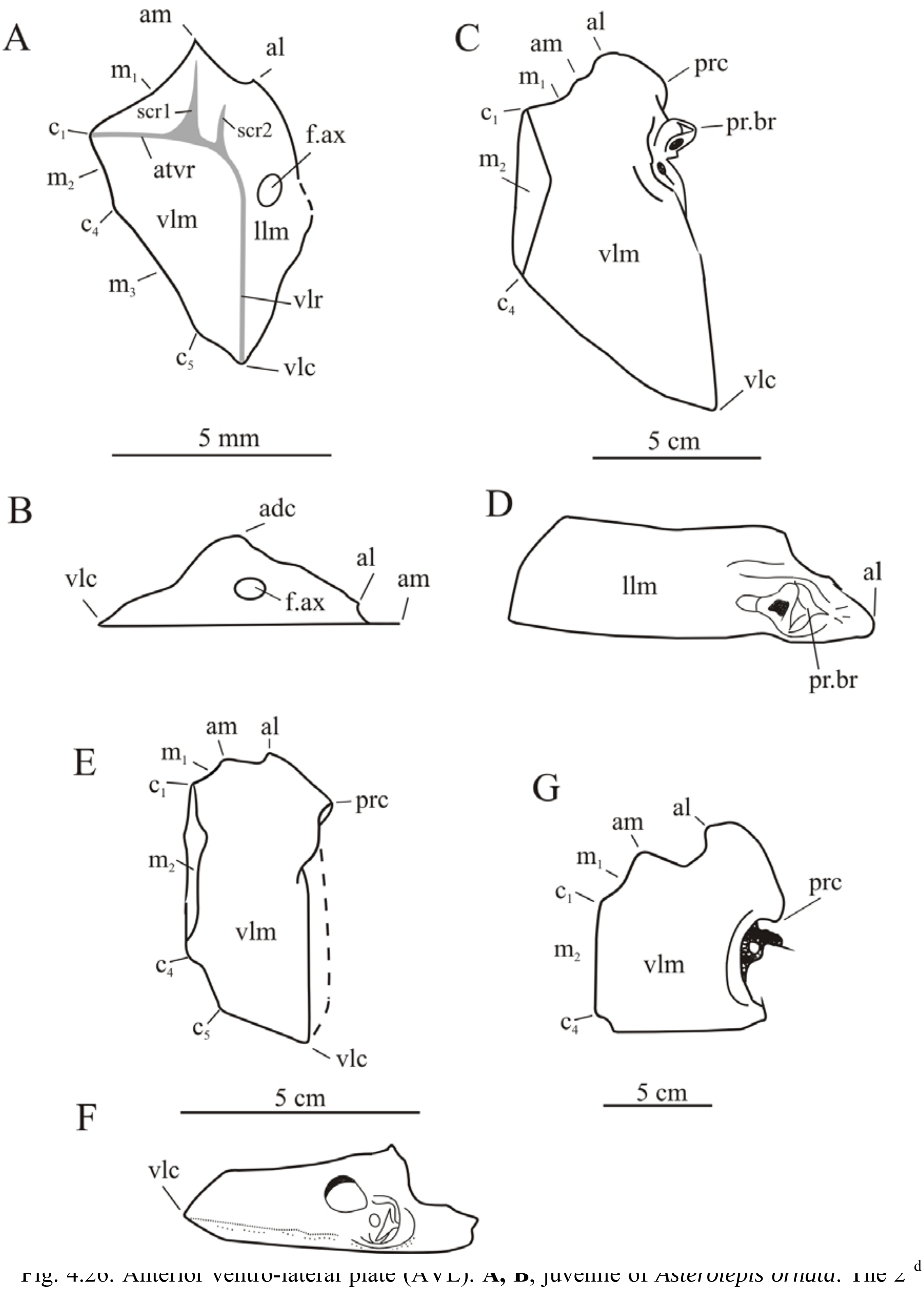


Fig. 4.26. Anterior ventro-lateral plate (AVL). **A, B**, juvenile of *Asterolepis ornata*. The 2d stage of ontogeny. LDM 260/476a,b, in external view. A, ventral and lateral lamina, mirror image; B, lateral lamina. **C, D**, adult of *Asterolepis ornata*, in external view (Karatajūte-Talimaa, 1963, Fig. 54), Upper Devonian, Latvia; C, ventral and lateral lamina; D, lateral lamina. **E, F**, adult of *Bothriolepis canadensis,* in external view. Upper Devonian, Canada; E, ventral and lateral lamina (Stensiö, 1948, Fig. 166 D), F, lateral lamina (Stensiö, 1959, Fig. 20 A). **G**, adult of *Remigolepis zhongningensis*, ventral lamina, in external view. Upper Devonian, China (Jiang *et al*., 1987, Fig. 29).

4.26. att.(iepr.lpp.) Priekšējā vēdera-sānu plātne (AVL). **A, B**, bruņuzivs *Asterolepis ornata* mazulim. Otrā ontoģenētiskās attīstības stadija. LDM 260/476a,b, ārskats. A, ventrālā un laterālā plakne, spoguļattēls; B, laterālā plakne. **C, D**, *Asterolepis ornata* pieaugušam īpatnim, ārskats (Karatajūte-Talimaa, 1963, Fig. 54), augšdevons, Latvija; C, ventrālā un laterālā plakne; D, laterālā plakne. **E, F**, bruņuzivs *Bothriolepis canadensis* pieaugušam īpatnim, ārskats. Augšdevons, Kanāda; E, ventrālā un laterālā plakne (Stensiö, 1948, Fig. 166 D), F, laterālā plakne (Stensiö, 1959, Fig. 20 A). **G**, bruņuzivs *Remigolepis zhongningensis* pieaugušam īpatnim, ventrālā plakne, ārskats. Augšdevons, Ķīna (Jiang *et al.*, 1987, Fig. 29).

The subcephalic part of the dorsal margin is well thickened and slightly produced upwards. The subcephalic division accounts for 41-46% of the total length of the ventral lamina, whereas reaching only 36% in adults (Gross, 1931, fig. 19. B). The ornamentation is concentric parallel to the subcephalic part of the dorsal margin (from the corner *am* to the level of the processus brachialis). The rest of the plate is covered with the ornamentation of fine-meshed network characteristic for juveniles or reticulate in advanced ones.

Foramen axillaris (f.ax) usually is well seen, it is oval in shape (Fig. 4.25. A,B; 4.26. A,B). The processus brachialis (pr.br) in juveniles is relatively shorter – its` shape is incompletely semilunar in the section. In adults it is relatively longer and is roundish in shape (Gross, 1940, fig. 7).

Posteriorly the AVL plate has a well-marked ventro-lateral corner (vlc) at the ventro-lateral ridge (vlr). The overlapped area for the PVL plate is triangular due to the sharp edged anterior margin of the PVL. It is contrary to that in adults where the mentioned overlapped area widely joins with the overlapped area of the PVL plate (Gross, 1931, Fig. 19. B).

The **posterior ventro-lateral** plate (PVL) comprises 4.35-10.50 mm in juveniles, 111.0-143.5 mm in adults. It exhibits considerable changes in shape and proportions during the growth of fish (Fig. 4.27.).

The ventral lamina is about four times as long as it is broad in the youngest individual, it comprises over than two and half to about three times in advanced ones, and almost twice in adults (appendix 2.20,. ratio: a/b). It is very narrow in the smallest known PVL plate (Fig. 4.27. A). During the growth it considerably broadens (ibid.: B-E) and exhibits developed antero-medial ($cm_1$) and middle corner ($cm_2$), as well as the anterior division of medial margin ($ma_1$) for participating in connection with the adjacent median ventral plate (MV). There is a posterior medial corner ($cm_3$) in juveniles, not preserved in adults (Figs. 4.3.; 4.4.; 4.27. C-E). It is rounded off on the left PVL plate, but protruded on the right PVL. The same is pointed out for adults of *Bothriolepis canadensis* (Stensiö, 1948, p. 333).

The ventral lamina of the left PVL plate is a little broader than that of the right PVL: the right one overlaps the left. The overlapped area exhibits finer reticulate ornament than that of the rest of the plate (Fig. 4.27. E). Protruded anterior corner (ac) on the *vlr* is overlapped by the AVL plate.

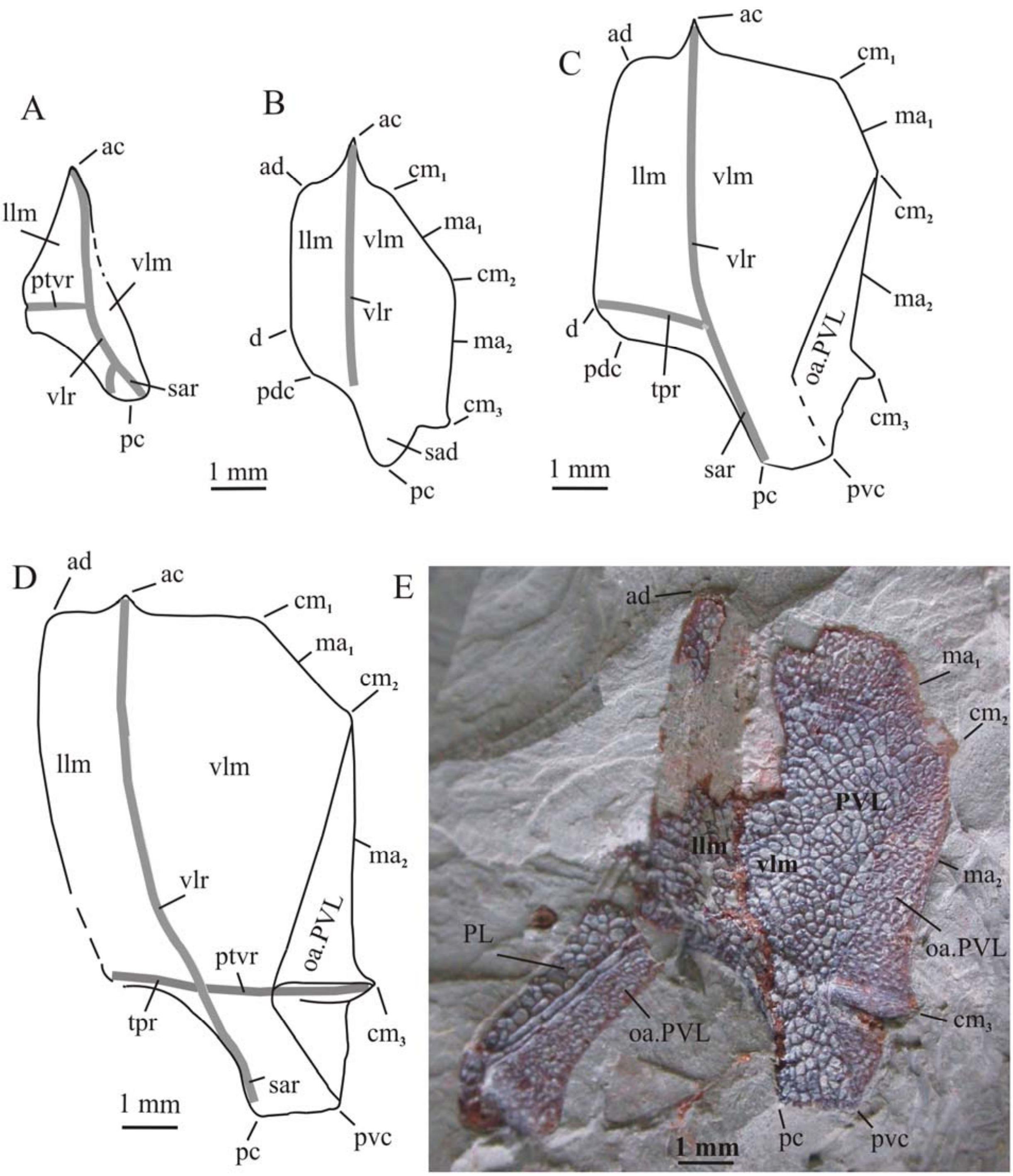


Fig. 4.27. Sequence of developmental stages of posterior ventro-lateral plate (PVL) of juveniles of *Asterolepis ornata*. **A,** left PVL, the 1st stage of ontogeny, mirror image, LDM 260/501, in external view. **B,** right PVL, the 2nd stage of ontogeny, LDM 260/502, in external view. **C,** right PVL, the 3rd stage of ontogeny, LDM 260/515, in external view. **D,** E right PVL, the 3rd stage of ontogeny, LDM 260/152, in external view (D-drawn from a part and a counterpart).

4.27. att. Bruņuzivs *Asterolepis ornata* mazuļa pakaļējā vēdera-sānu kaula (PVL) attīstības stadijas. **A,** kreisais PVL, pirmā ontoģenētiskās attīstības stadija, spoguļattēls, LDM 260/501, ārskats. **B,** labais PVL, otrā ontoģenētiskās attīstības stadija, LDM 260/502, ārskats. **C,** labais PVL, trešā ontoģenētiskās attīstības stadija, LDM 260/515, ārskats. **D,** E labais PVL, trešā ontoģenētiskās attīstības stadija, LDM 260/152, ārskats (D-kombinēts zīmējums no abām parauga pusītēm).

The lateral lamina is about three times as long as it is broad, whereas five times in adults (Lyarskaya, 1981, p. 118). The lateral lamina is highest at the dorsal corner (d), as in adults (Lyarskaya, 1981, fig. 87-3). In some specimens this corner is well rounded off. The height of the lamina decreases forward from its dorsal corner, as in adults. During the growth the width of the anterior part of the lateral lamina increased from about one fourth to about one and to about one half 4.33-1.16-1.79 (Fig. 4.27. A-C; appendix 2.20., ratio: $c/c_1$). The width of its` posterior part does not exhibit remarkable changes during the ontogeny comparing juveniles and adults (appendix 2.20., ratio: a/c). The postero-dorsal corner (pdc) usually is well pointed but may be also obtuse (LDM 260/506, 260/515).

The subanal division (sad) of the plate accounts about one third (Fig. 4.19.) as in adults (Lyarskaya, 1981, fig. 87-3). It is convex in smallest juveniles (Figs. 4.4.; 4.27. A,B) with rounded posterior corner (pc); in advanced juveniles it becomes stout with almost straight posterior margin and developed postero-ventral corner (pvc) (Fig. 4.27. C-E) as in adults (Fig. 4.3. A). The subanal ridge (sar) as the prolongation of the ventro-lateral ridge (vlr) crossed the division along its` concave postero-lateral margin (Figs. 4.4.; 4.27.). There is an additional very small-unnamed ridge beside the subanal ridge (sar) on the subanal division of the smallest known PVL plate (Fig. 4.27. A), not observed in later stages of growth of fish. Presumably, the numerous and various ridges strengthened the dermal armour when it was very thin, as mentioned before.

Medially the PVL plate overlaps the PL plate, in adults the MxL plate.

The **median-ventral (MV)** plate in juveniles is rhomboidal with rounded corners (Fig. 4.28. D). The plate is usually longer than broad, in some specimens only slightly. The anterior and posterior halves in juveniles are of equal length, in adults this ratio is slightly variable: both of equal length (Fig. 4.28. E), or the anterior half is slightly longer (Fig. 4.34.C).

The MV plate started to ossify when another armour plates of the body had been already completely ossified. So, the smallest juvenile individuals (ontogenetic stage 1 and 2; the length of the ventral wall 11.3-11.7 mm) exhibit rhomboidal unossified area (Fig. 4.28.A) in the place of subsequently later ossifying MV plate. The uncovered area is relatively large to compare with that of the older juveniles with initial development of the MV plate. Presumably, it is due to the rather straight medial margins of the adjacent AVL and PVL plates in the youngest juveniles. Mentioned margins became more convex with the growth, and consequently the MV plate looks relatively smaller in the advanced individuals.

The basal layer of bone forming the MV plate starts to appear in juveniles with the total length of the ventral wall 12.1-13.2 mm (ontogenetic stage 2). The basal layer is well marked and translucent (Fig. 4.28. B,C). The three layered bone structure of the MV plate appears in juveniles (Fig. 4.28. D), whose total length of the ventral wall is 16.5-17.2 mm (ontogenetic stage 3). The reticular ornament appears on the exposed rhombic non-overlapping area. The overlapped areas for the AVL and PVL plates are smooth and well developed.

In adults the MV plate is rather roundish; it has a well-pronounced rhombic tubercular ornamented area (Figs. 4.28. E; 4.34. C). The ratio of the length/breadth of the MV plate shows no allometry: in juveniles and adults it comprises about 1.1 (appendix 2.18.: a/b). Therefore the ventral wall of juveniles looks like more slender than that in adults, where it appears rather stout.

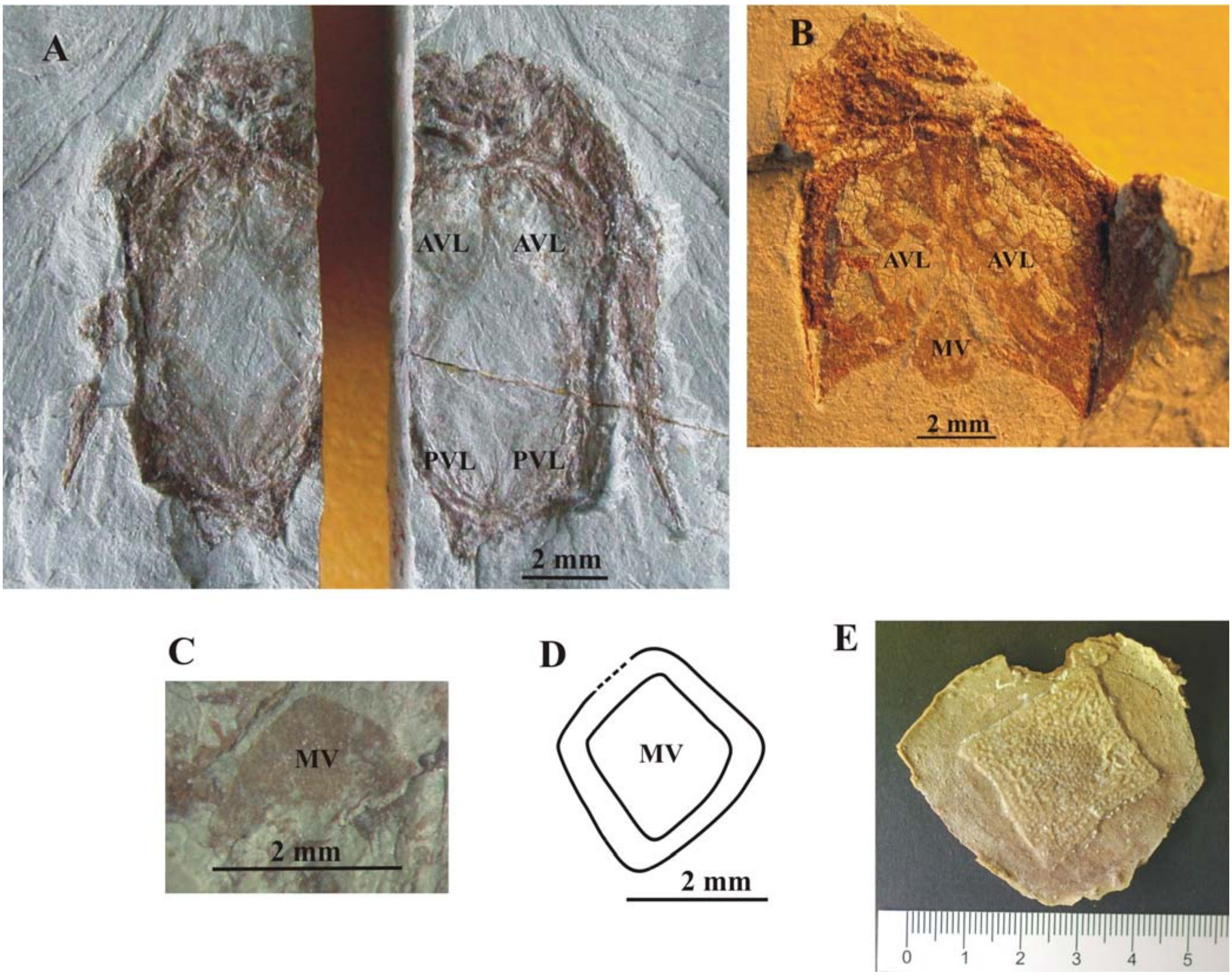


Fig. 4.28. **A-D**, Sequence of developmental stages of the median ventral (MV) plate of juveniles of *Asterolepis ornata*. **A,** ventral wall with ventral fontanel, a part and a counterpart. LDM 260/7ab, in visceral view (Upeniece, Upenieks, 1992, Pl.1, fig. 1). **B,** anterior part of the ventral wall; MV is initially developed, translucent, without ornamentation and roundish, LDM 260/237a, in visceral view. **C,** fragment of the MV plate; translucent, without ornamentation, LDM 260/94a, in visceral view. **D,** MV plate with the developed ornamented and overlapped areas, LDM 260/153b. **E**, MV plate of adult of *Asterolepis ornata*, LDM G 291/89, in external view.

4.28. att. **A-D**, Bruņuzivs *Asterolepis ornata* mazuļa vidējās ventrālās bruņu plātnes (MV) attīstības stadijas. **A**, vēdera sieniņa ar ventrālo atvērumu, abas parauga puses. LDM 260/7ab, iekšskats (Upeniece, Upenieks, 1992, Pl.1, fig. 1). **B**, vēdera sienas priekšējā daļa; MV plātne ir sākotnējā attīstības stadijā, caurspīdīga, bez ornamentējuma, ieapaļas formas, LDM 260/237a, iekšskats. **C**, MV plātnes fragments, bez ornamentējuma, LDM 260/94a, iekšskats. **D**, MV plātne ar attīstītu ornamentējumu un pārklājumu malām, LDM 260/153b. **E**, MV plātne pieaugušam īpatnim *Asterolepis ornata*, LDM G 291/89, ārskats.

Table 4.2. Measurements and indices of the median ventral (MV) plate
in juveniles and adults of *Asterolepis ornata*

4.2. tabula. Medio ventrālās bruņu plātnes (MV) izmēru un proporciju salīdzinājums bruņuzivju
*Asterolepis ornata* mazuļiem un pieaugušajiem īpatņiem

| Stage of onto-geny | Presence of MV plate | Length/ breadth of ornamented area of MV plate, mm | Ratio: length / breadth of MV plate | Length of ventral wall, mm | Ratio: length of MV plate (exposed area) / length of ventral wall | Specim. No LDM |
|---|---|---|---|---|---|---|
| II | no ossified | -<br>**3.2/2.5** | -<br>**1.3** | 11.3 | 0.28 | 260/7 |
| II | initial ossification - only basal layer developed | -<br>**3.8/3.0** | -<br>**1.3** | 13.2 | 0.29 | 260/100 |
| Adult* | ossified plate | ~ 72.0/68.0 | 1.1 | 264 | ~0.27 | 60/91 |
| Adult* | ossified plate | 88.0/68.0 | 1.3 | ~312 | 0.28 | 60/48 |

* - Estimated measurements after Lyarskaya (1981, figs. 76, 77).
**In bold** - measurements of unossified area or of developed initial ossification. The area coincides with the ornamented area of MV plate in adults.

The ratio between the lengths of the exposed area of the MV plate (without overlapped areas) and the whole ventral wall remains constant: it is about 0.28 in juveniles and adults (Table 4.2.). So, no allometry is observed during the growth between these characters.

It is important to note, that there is uncovered ventral fontanel in early ontogenetic stages of antiarch *Bothriolepis* sp. as well, reported in Criswell et al. (2007) and Downs et al. (Figs. 2, 5, 8a; in press, 2011).

The paired **semilunar (Sm)** plate in juveniles is well preserved. The shape of the Sm plate is more typical semilunar in juveniles than in adults: the anterior margin is more concave and posterior one is more convex (Fig. 4.29. A-C). The antero-lateral corner (alc) of the plate is extended – it has a more height position and is rather pointed in contrary to that in adults. The anterior corner (ac) is pointed, in adults it is rounded off and is very weakly pronounced. The well developed anterior corner, as well as the rather high position of the anterior-lateral corners are noted for the related antiarch *Pterichthyodes* (Fig. 4.29. D).

The Sm plate in juveniles and adults is about half times as long as broad (see appendix for Sm plate, a/b). The ratio between the lengths of the medial margin (a) to the height of the anterior-lateral corner ($a_1$) in juveniles comprises 0.59-0.68, in adults 0.73 (ibid., $a/a_1$). So, with the growth the antero-lateral corner slowly had been become lower.

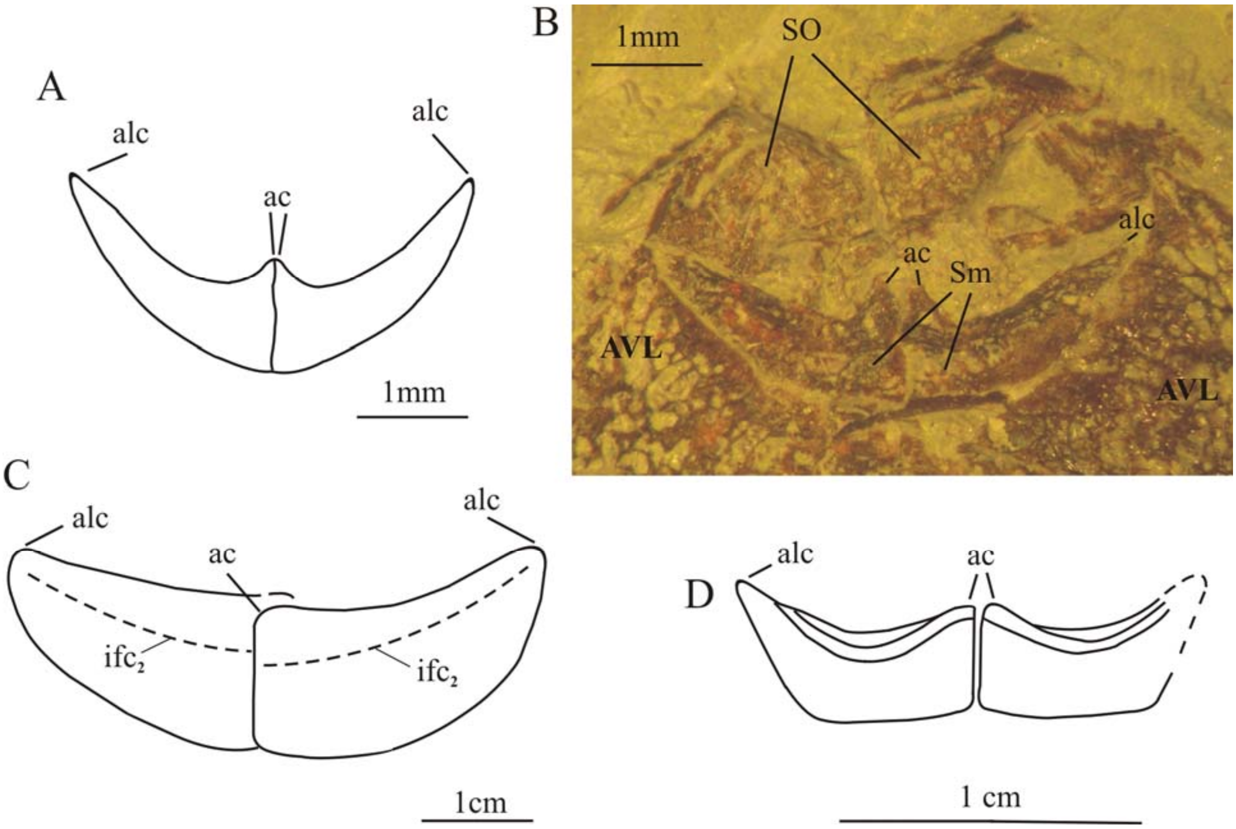


Fig. 4.29. Semilunar plate (Sm). **A, B** of juvenile of *Asterolepis ornata.* A, visceral side. LDM 260/239. B, external side. LDM 260/1. **C**, of adult of *Asterolepis ornata*, external side. UP 10/1-1. **D**, of *Pterichthyodes milleri,* ventral view (Hemmings, 1978, fig. 17 A).

4.29. att. Pusmēness kauls (Sm). **A, B** bruņuzivs mazulim *Asterolepis ornata.* A, LDM 260/239, iekšskats. B, LDM 260/1, ārskats. **C**, pieaugušam īpatnim *Asterolepis ornata*, UP 10/1-1, ārskats. **D**, bruņuzivij *Pterichthyodes milleri*, ārskats (Hemmings, 1978, fig. 17 A).

### 4.1.7. Pectoral fins

Pectoral fin is relatively long and slender in juveniles, whereas in adults of *Asterolepis* it is short and broad (Lyarskaya, 1981, fig. 31), as in other asterolepidoids. Pectoral fin (Fig. 4.3.) almost reaches the posterior end of the trunk shield in juveniles. On the contrary to that in adults the length of the pectoral fin comprises two thirds of the trunk armour. The bones of the fin segments demonstrate typical serratiform suture by means of minute sharp spines in juveniles (Fig. 4.30. A-D). There are traces of denticles on suture faces in adults of *Asterolepis* (ibid.: E,F). The longitudinal ridge stretches along the middle line on the dorsal side of the pectoral fins in juveniles (pfr, Fig. 4.4. A). It is not well visible on the ventral side.

Unlike the conditions in adults of *Asterolepis*, the distal segment in juveniles is composed of two dorsal and two ventral central plates (Figs. 4.4.; 4.31. A-C), resembling conditions in adults of *Bothriolepis* (Stensiö, 1948) and *Pterichthyodes* (Hemmings, 1978, fig. 18). In the later stages of the development the terminal plate in juveniles must have been accreted to the nearest – the second central plate to form the $Cd_3$ plate in adults, but no sutural lines are visible between them in adult individuals of *Asterolepis ornata* (Fig. 4.31. D, E). There is an additional $Ml_5$ plate in the distal segment in juveniles judging from the shape of the terminal plate (Fig. 4.31. A, B).

It is important to note that the number of dermal plates in the pectoral fin in juveniles of *Asterolepis* coincides, for example, with that of the Middle Devonian antiarchs *Pterichthyodes milleri* (Fig. 4.31. F) or *Byssacanthus dilatatus* (Karatajūte-Talimaa, 1960, fig. 3) and not with that in adult of *Asterolepis ornata* (Figs. 4.3.; 4.4.; 4.31. D, E). The genus *Asterolepis* is the only one who possesses the one central plate in the distal segment.

The medial and lateral rows of spines are well developed contrary to that in adults: spines are numerous, sharp and flattened in section. In adults these spines are less marked: they are considerably smaller, with rounded tips and more circular in section (Fig. 4.30. D). Similar developmental pattern of the rows of spines such as stronger appearance of spines in young individuals than in older and mature ones is known also for *Bothriolepis* species (Stensiö, 1948, p. 153).

The length of the pectoral fin varies from 3.5 mm in the youngest articulated individual (Fig. 4.43. B) to 15.0 mm in the oldest juvenile (Fig. 4.47.). The length of the distal segment, in contrast to that in adult *Asterolepis ornata,* is greater than the length of the proximal segment; the ratio is 0.57-0.88, but with the growth of the fish they tend to become more uniform in their length. In the older juvenile the ratio is 0.9, as it is in adults. The distal end of the pectoral fin is remarkably sharp.

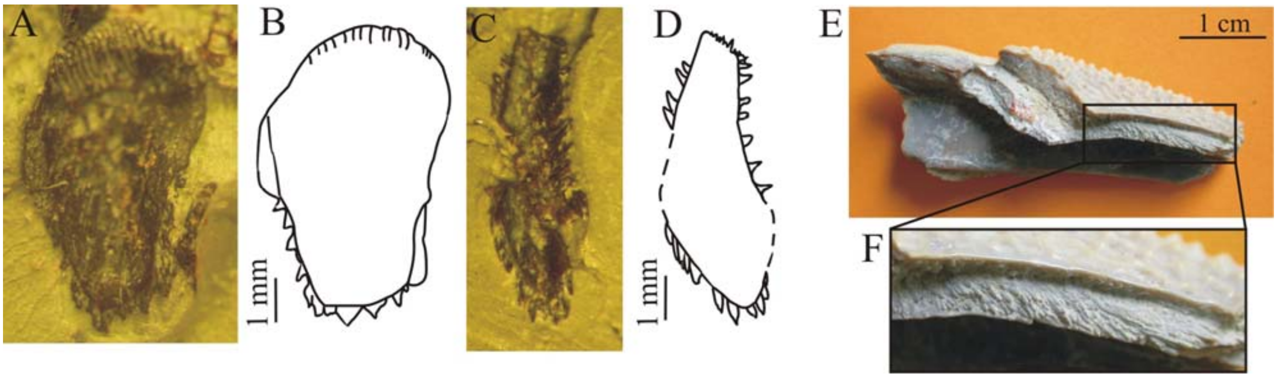


Fig. 4.30. Pectoral fin plates of *Asterolepis ornata* with preserved serratiform sutural connections: of juvenile individuals (**A-D**), of adult (**E, F**). **A, B**, ventral central plate 1 ($Cv_1$), in visceral view. LDM 260/152b. **C, D**, mesial marginal plate 2 ($Mm_2$), in visceral view. LDM 260/152a. **E, F**, lateral marginal plate 3 ($Ml_3$), in external view. UP 10/1-6.

4.30. att. Krūšu peldspuras bruņu plātnes brunuzivij *Asterolepis ornata* ar zobiņveida sutūru savienojumiem: mazuļiem (**A-D**), pieaugušiem īpatņiem (**E, F**). **A, B**, krūšu spuras pirmais centrālais vēdera kauls ($Cv_1$), iekšskats. LDM 260/152b. **C, D**, krūšu spuras otrais sānu vidējais kauls ($Mm_2$), iekšskats. LDM 260/152a. **E, F**, krūšu spuras trešais sānu malas kauls ($Ml_3$), ārskats. UP 10/1-6.

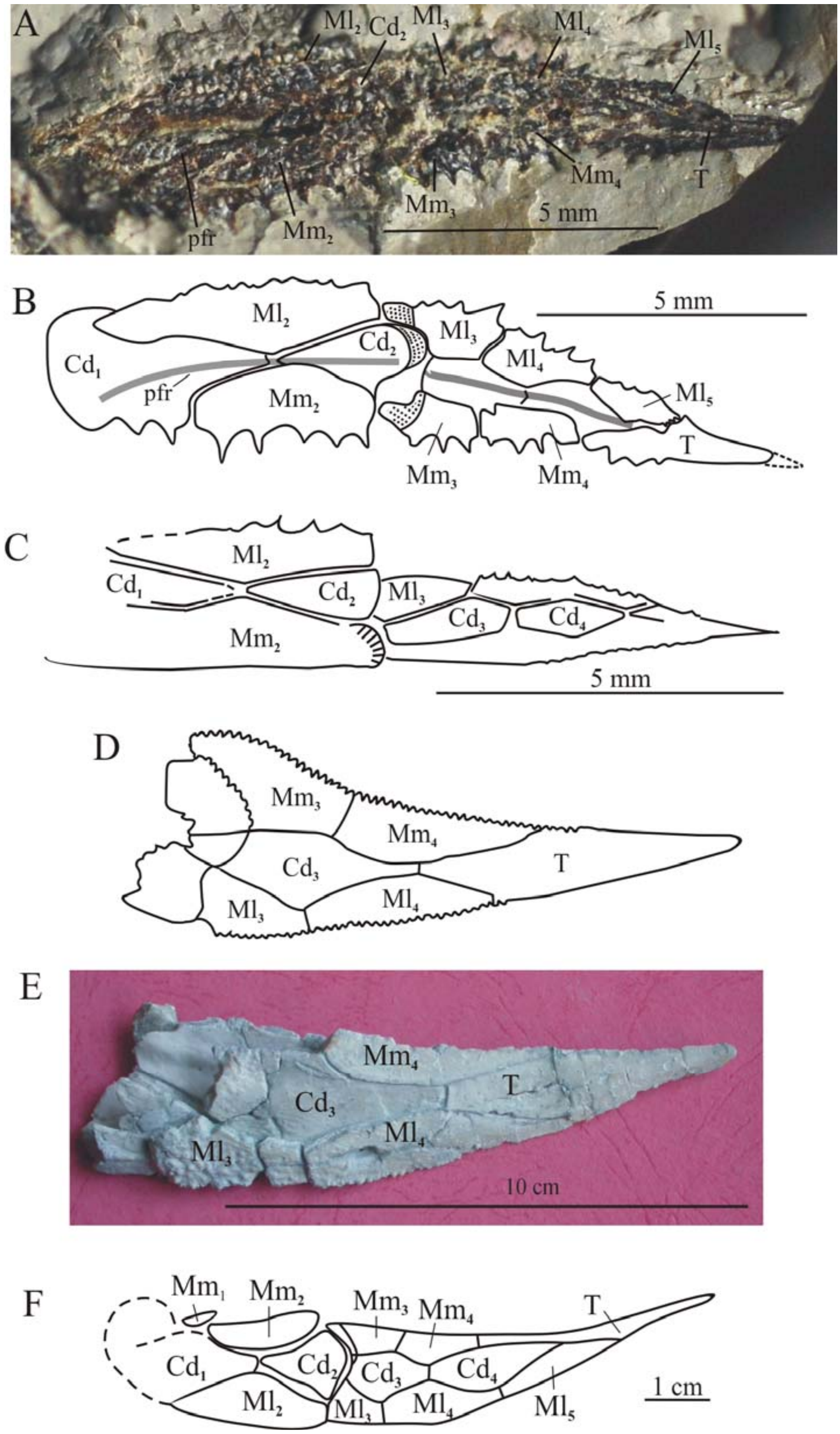


Fig. 4.31. **A-C.** Pectoral fin of juvenile *Asterolepis ornata*. A, B, LDM 260/301a, in external view. C, LDM 260/222b, in visceral view. **D, E**. Distal segment of the pectoral fin of adult *Asterolepis ornata*. D, after Gross (1931, Pl. VI, Fig. 3). E, UP 10/1-2. Lode quarry. **F**, Pectoral fin of adult *Pterichthyodes milleri,* Middle Devonian, Scotland (Hemmings, 1978, fig. 18 A).

4.31. att. **A-C.** Krūšu peldspura bruņuzivs *Asterolepis ornata* mazulim. A, B, LDM 260/301a, ārskats. C, LDM 260/222b, iekšskats. **D, E**. Krūšu peldspuras distālais segments *Asterolepis ornata* pieaugušam īpatnim. D, pēc Gross (1931, Pl. VI, Fig. 3). E, UP 10/1-2. Lodes karjers. **F**, Krūšu peldspura bruņuzivij *Pterichthyodes milleri,* vidusdevons, Skotija (Hemmings, 1978, fig. 18 A).

### 4.1.8. Types of sutural connections

The dermal skeleton of placoderms occurs in two main divisions: the skeleton of the tail and trunk division behind the armour consists of numerous diamond-shaped scales, while the head and trunk armour skeleton is united into two capsules composed of a number of large plates united by various joints; in antiarchs pectoral fins also were covered by dermal ossifications. All three types of sutural connections characteristic for vertebrate skeletons in accordance with the functional classification (FCAT, 2000) have been recognised within the skeleton of juvenile and adult *Asterolepis ornata*: 1) immovable joints (synarthrodial) between all plates of the trunk armour and most part of the plates forming the head shield, as well as between plates forming the proximal and distal segments of the pectoral fin skeleton; 2) slightly movable joints (amphiarthrodial), such as connections between the lateral and submarginal plates, and some other joints; 3) fully movable joints (diarthrodial) between the head shield and trunk armour, between the trunk armour and the pectoral fin, as well as between the proximal and distal segments of the pectoral fin. According to the structural classification (ibid.), the main part of sutural connections in *Asterolepis* corresponds to the type of fibrous joint; some could be regarded as cartilaginous joints, e.g., the joint between the lateral and submarginal plates, as well as between the postpineal and pineal plates; the joint between the trunk armour (AVL plate) and pectoral fin corresponds to the type of synovial joint.

The sutures corresponding to the type of fibrous joint are usually subdivided further into squamous, smooth, and serratiform suture; sometimes the so-called oblique smooth suture also has been distinguished. According to the modern terminology, the squamous suture is a suture whose opposing margins are scale-like and overlapping; the smooth suture is a suture whose opposing margins are perpendicular to the outer and inner surface of the contacting plates, which are not overlapping; the serratiform suture is a serrated connection between the two plates. Such type of sutural connection as gomphosis, when one bone fits into another bone like mammal tooth fits within the jaw, is rarely observed in placoderms.

Fibrous joints in vertebrates usually are immovable in adults, but allow some degree of movements during the early stages of ontogeny, therefore the study of changes of sutural connections between plates during growth of *Asterolepis* is of high importance. Only some authors paid attention to this question previously. V. Karatajūte-Talimaa distinguished two kinds of the sutural connections in the skull of adults of *Asterolepis*: “obliquely overlapped” and the so-called “suture in harmony” (Karatajūte-Talimaa, 1963, p. 89), or oblique smooth suture and smooth suture in accordance with the modern nomenclature. The oblique smooth suture, for example, joins the nuchal and postpineal in adult individuals, although it exhibits some peculiarities, discussed below.

The most of the head-shield plates in juveniles have serratiform connections (Figs. 4.32. A-E; 4.33. B). Serratiform suture is best observable in the disarticulated or slightly deformed specimens, and it has been found between the following plates of the dermal head shield of juvenile *Asterolepis* (Upeniece, 2005): lateral and nuchal, lateral and paranuchal, lateral and postpineal, nuchal and postpineal, nuchal and paranuchal. The sutural connection between the paranuchal and postmarginal plates is of the smooth type of fibrous joint, or “in harmony” in accordance with nomenclature of Karatajūte-Talimaa. The submarginal plate, which does not belong to the head shield, is connected with the premedian plate through the cartilaginous joint.

The serration within the joints has changed remarkably during the ontogeny. Numerous irregular and flat denticles form the serratiform suture (Figs. 4.12. C,D; 4.32. A-

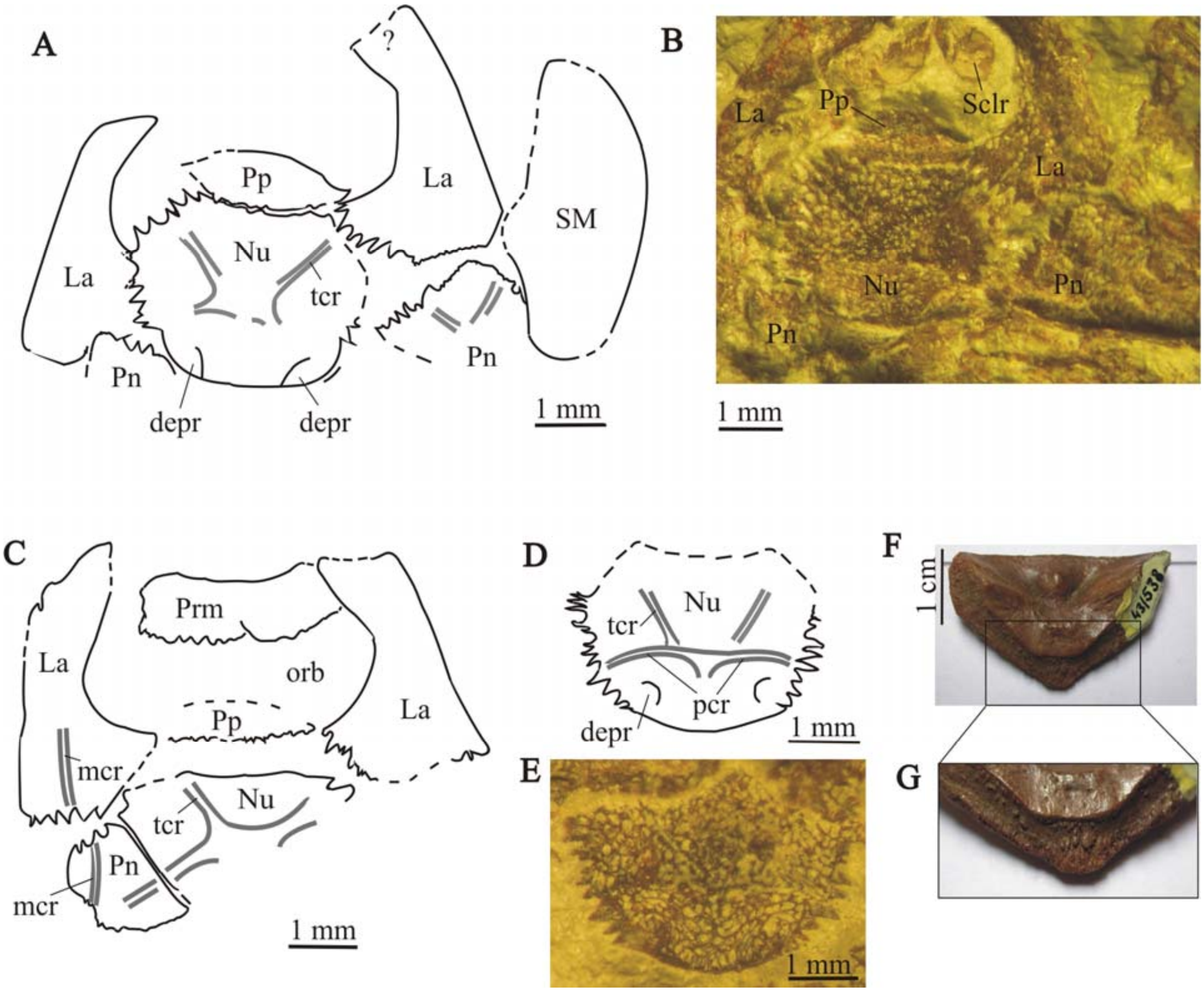


Fig. 4.32. Types of sutural connections between the head-shield plates of *Asterolepis ornata*. **A-E**, Serrated connection type in juvenile individuals, in external view. **A, B,** detached head plates LDM 260/5. C, detached head plates LDM 260/193. **D, E,** nuchal plate LDM 260/250. **F, G**, Oblique serratiform suture of adult. Pineal plate, in visceral view, with some preserved denticles. LDM 43/538.

4.32. att. Sutūrsavienojumu veidi starp galvas vairoga bruņu plātnēm bruņuzivij *Asterolepis ornata*. **A-E**, Zobiņveida savienojumu veids mazuļiem, ārskats. **A, B,** atdalījušās galvas bruņu plātnes LDM 260/5. C, atdalījušās galvas bruņu plātnes LDM 260/193. **D, E,** pakauša kauls LDM 260/250. **F, G**, Slīpais zobiņveida savienojumu veids pieaugušam īpatnim. Pineālais kauls, iekšskats, saglabājusies daži zobiņi. LDM 43/538.

E) in the smallest juveniles with the 14-16 mm long head plus dorsal trunk armour (2nd stage of ontogeny). The serratiform suture becomes more regular, with more rare denticles, which are roundish in the cross section (Fig. 4.12. E), in slightly larger juveniles characterised by the dermal plates with the developed three-layered bone structure (3rd ontogenetic stage).

Opposite to juvenile individuals, the head shield of adults of *Asterolepis* show mainly almost smooth contact surfaces with some preserved denticles, which could be treated as the remnants of the serratiform sutural connections. The connection between the nuchal and postpineal plate (Fig. 4.32. F, G) presumably would be treated as the transitional, the oblique serratiform suture, due to appearance of preserved denticles on the oblique smooth suture.

Unlike the sutures between the plates of the trunk armour, the suture between the nuchal and postpineal plates is only slightly oblique and hence the overlapping area is much narrower than the overlapping areas on the plates of the trunk armour, so this suture cannot be treated as the typical squamous suture. Small denticles pointing to the serratiform connection have been observed also in the contact area on the nuchal and lateral plate. Such bones of the head skeleton of adult *Asterolepis* as pineal and rostral plates were most probably connected to the rest of the plates of the head through the cartilaginous joint (see also Karatajūte-Talimaa, 1963, p. 90), whereas the suture between these two bones is presumably of the smooth fibrous type of connection.

The dermal plates of the pectoral fin of *Asterolepis ornata* demonstrate the serratiform sutures in juveniles and with traces of preserved denticles in adults. Plates of the pectoral fin in adult *Asterolepis* show very well developed serratiform sutures: denticles forming the connection are better pronounced in comparison with the head shield, they have been traced on the contact surfaces of the $Cv_1$ plate where it sutures with the $Ml_2$ plate (specimen LDM 43/504), as well as on the $Ml_3$ plate (Fig. 4.30. E,F). In juveniles the plates in the proximal and distal segment of the pectoral fin have serratiform sutural connections (Figs. 4.30. A-D; 4.31. A-C). The serration superficially resembles the appearance of the outer lateral spine row of pectoral fin of *Bothriolepis*, but denticles are much smaller.

The trunk armour plates of both juveniles (Figs. 4.21. A-D; 4.22. A; 4.23. E; 4.27. E) and adults of *Asterolepis ornata* (Figs. 4.21 F; 4.22. C,D; 4.24. I,J; 4.28. E; 4.34.) were connected through the squamous sutures (or overlapping type sutures). The development of these structures is well traceable in individuals belonging to the 2nd and 3rd stages of ontogeny; this is further discussed in the chapter 4.2.3. Most probably, squamous suture provide wider connection between the relatively thin and rather wide and long plates of the trunk armour thus being more effective than the serratiform suture hence providing mechanically firm construction protecting the internal organs of fish.

Comparison of sutural connections between various bones of the head, pectoral fin and trunk armour lead to suggestion that the serratiform sutures even after death of individual provided stronger connections between relatively thick and small plates than the squamous sutures typically connecting relatively thin plates with large surface. The relative strength of the sutural connections of different types can be best evaluated observing the sequence of disintegration of the armour of adult *Asterolepis ornata* (Upeniece, 1999): after the disconnection of the tail and the head from the rotting corpse, plates of the trunk armour became easily disconnected pointing to the relatively weak connection through the squamous suture strengthen by connective tissue in living fish. Contrary to the trunk armour, the complete head shields and pectoral fins consisting of the plates connected with the serratiform sutures still are frequently found long after disintegration of the trunk armour. In juveniles the disintegration of the head starts with disconnection of suborbital plate most probably connected to the shield with the cartilaginous joint, and postmarginal and premedian plates demonstrating almost smooth sutures. Only then those head plates, which are located around the endocranium and connected with strongly developed serratiform sutures, were disconnected.

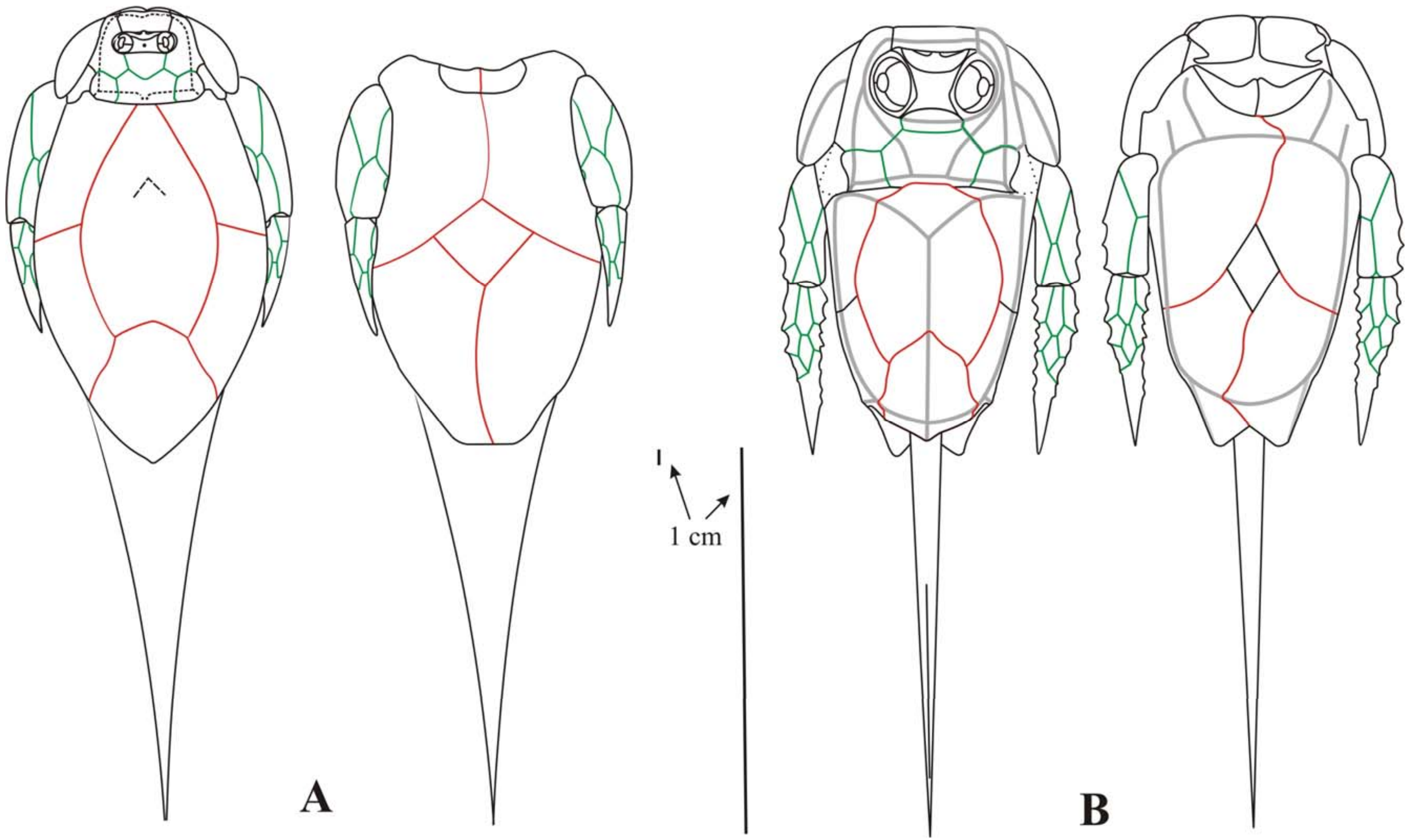


Fig. 4.33. Types of sutural connections between the armour plates of *Asterolepis ornata*. Green lines indicate serratiform connections (of pectoral fins and partly of the head-shield), red lines – connections of squamous (overlapped) type (dorsal and ventral walls of the trunk armour). **A,** adult (after Lyarskaya, 1981, Fig. 74, with slight modifications in semilunar area). **B**, juvenile (Upeniece, Upenieks, 1992, Figs. 2B, 3B, with slight modifications in semilunar area).

4.33. att. Sutūrsavienojumu veidi starp bruņu plātnēm bruņuzivij *Asterolepis ornata*. Zaļās līnijas ir zāģveida savienojumi (krūšu peldspurām un daļēji galvas vairogam), sarkanās līnijas – zvīņveida savienojumi (pārklājumi) (rumpja muguras un vēdera sienām). **A,** pieaudzis īpatnis (pēc Lyarskaya, 1981, Fig. 74, ar nelielām izmaiņām pusmēness kaula reģionā). **B**, mazulis (Upeniece, Upenieks, 1992, Figs. 2B, 3B, ar nelielām izmaiņām pusmēness kaula reģionā).

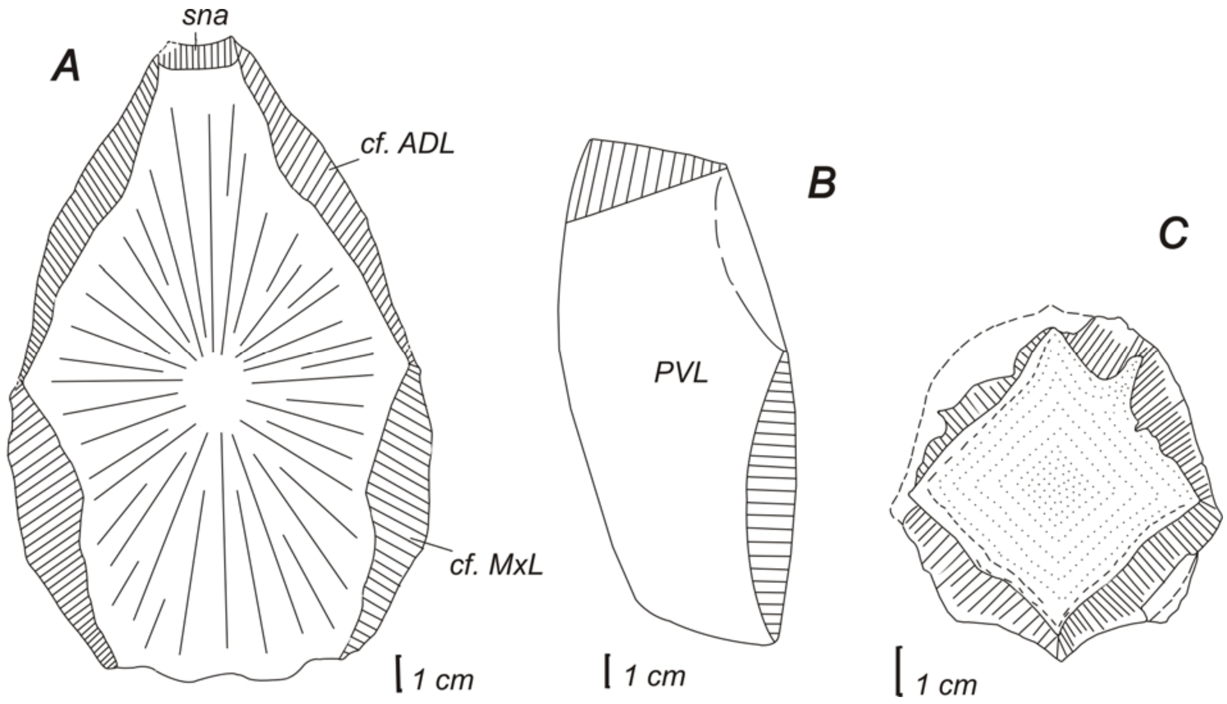


Fig. 4.34. Squamous (overlapped) type of suture in adults of *Asterolepis ornata*. A, anterior median dorsal plate (AMD) UP 10/1-3, in visceral view. B, posterior ventro-lateral plate (PVL), in visceral view (Lyarskaya, 1981, fig. 87-1). C, median ventral plate (MV), in external view (Lyarskaya, 1981, fig. 88).

4.34. att. Zvīņveida (pārklājumu) sutūrsavienojumu veids pieaugušām brunuzivīm *Asterolepis ornata*. A, priekšējā vidējā muguras plātne (AMD) UP 10/1-3, iekšskats. B, pakaļējā vēdera-sānu plātne (PVL), iekšskats (Lyarskaya, 1981, fig. 87-1). C, vidējā ventrālā plātne (MV), ārskats (Lyarskaya, 1981, fig. 88).

The serratiform sutures characteristic for the head shield of juveniles of *Asterolepis* have not been described for young individuals of antiarch *Bothriolepis* (Young, 1988, text-fig. 19), but are visible between the plates of the pectoral fin in presumably juvenile specimens of the `asterolepidoid` figured by Young (1984b, figs. 5-7). Serratiform sutures similar to those of juvenile *Asterolepis* have been observed on the internal mold of juvenile specimen of *Chuchinolepis gracilis* in the course of studies of Chinese antiarchs hold at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing. The above-mentioned mold has been illustrated but not commented by Zhu (1996, Fig. 20 A); this specimen reveals typical serration on the posterior margin of the postpineal plate, posterior lateral margin of the lateral plate and anterior margin of the paranuchal plate. Similar distribution of different types of sutures between plates in various groups of antiarchs suggests that the type of sutural connection is strongly determined by the mechanical requirements to the particular part of the dermal armour and the proportions of the contacting bones. Strongly developed serratiform sutures may serve as one of the best indicators of immaturity of individuals of placoderm fishes, but this suggestion should be approved by further studies of small individuals belonging to various antiarch taxa.

### 4.1.9. Squamous part of the body

The **squamation** in juveniles of *Asterolepis* is fairly commonly preserved and consists of bony scales. The tail is heterocercal and bears a single dorsal fin as in adults (Fig. 4.19.). The squamous (caudal) part of fish young comprises an almost half of the total body length (Fig. 4.3.). In adults it comprises little less than half - reaching about two fifths of the total body length (Ivanov *et al.*, 1996, fig. 4 A, Table 1).

The preserved squamation in juveniles comprises both fulcral and flank scales. Scales decrease in size caudally (Fig. 4.35.). The squamation or part of it is preserved in 33 juveniles. The **film of skin** is preserved in the smallest juveniles: the lateral side of the squamous part directly behind the posterior aperture of the trunk armour is covered with the brownish stain instead of the scale covering (Fig. 4.35. D), whereas the dorsal and ventral sides of the mentioned region are covered with the minute scales; they are much smaller to compare with those in the middle part of the tail.

The complete length of the tail in the juvenile material available is 0.99 – 1.61 cm. The maximal length of the tail in adults may reach 30 cm (Lyarskaya, 1981, p. 119); however, Ivanov et al. (1996, Table 1) mentioned that the length of the tail in adults varies from 14.0 to 25.5 cm. The maximal height of the laterally compressed tail in juveniles comprises about 0.19-0.24 cm. Zones of squamation in juveniles are not visible, contrary to what is described for the adults of *Asterolepis ornata* (Ivanov *et al.*, 1996, fig.5). The main lateral line canal in juveniles is not observed. In adults it is remarkable and well imprinted on the scales (ibid.: figs. 1, 6 F).

There is no evidence of pelvic fins neither in juveniles nor in adults. Nevertheless, an unclear imprint of that could be pointed out for juvenile in one specimen (Fig. 4.35. D, E) which might be either an unknown simetrical element (? remains of the pelvic fin girdle) or peculiar result of fossilization.

**Scales** of *Asterolepis* juveniles morphologically differ from these in adults (Fig. 4.36. D,E), having a different shape and surface structure: they have a thin lamina at the base with one tubercle on the dorsal surface, corresponding to a pit on the visceral surface (Upeniece, Upenieks, 1992, fig. 4; Ivanov *et al.*, 1995, Pl.1, figs. 1-6; 1996, fig. 8 K-M; Upeniece, 2001, 2006). The lamina consists of a compact bony tissue similar to that of the trunk armour plates. So, each scale carries a posteriorly directed tubercle. The tubercle is conical (maximal height 0.25 mm) with more or less rounded tip. The tubercle is composed of loose tissue with small canal openings (Ivanov *et al.*, 1995).

The scales in juveniles are without an evident overlap area. Each scale of adult *Asterolepis* carries an overlap area for three preceding scales; the scales are flat and the bigger ones possess the ornamentation of small tubercles (Lyarskaya, 1981, fig. 89; Ivanov *et al.*, 1996, fig. 6).

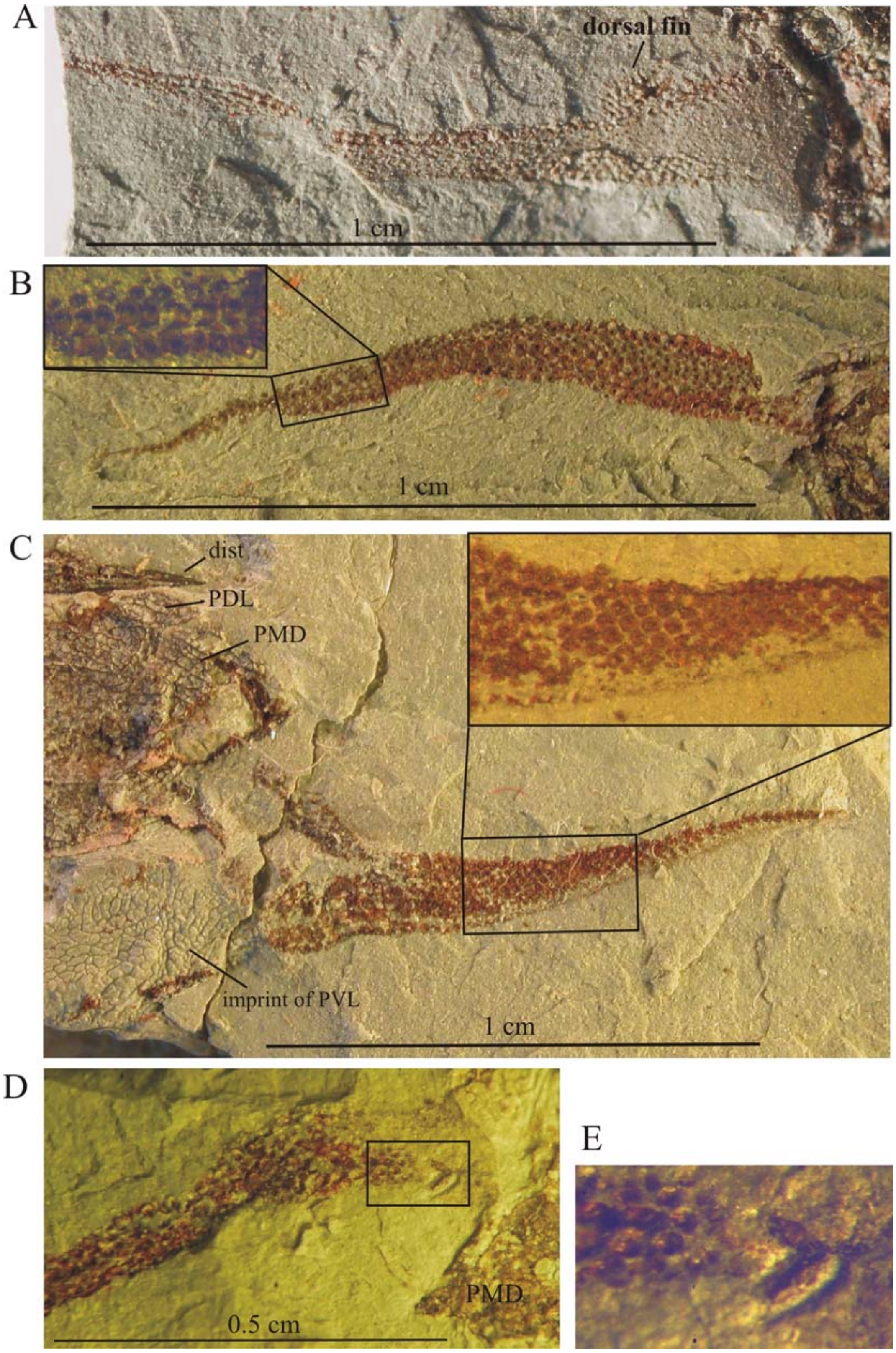


Fig. 4.35. Squamous part of juvenile *Asterolepis ornata*. **A,** with preserved dorsal fin. LDM 260/80a, in visceral view (scales with tubercle are in external view) (Upeniece, Upenieks, 1992, Pl.4, fig. 4). **B,** LDM 260/235a, in visceral view. Fulcral scales are shown in detail. **C,** LDM 260/88a, in visceral view. Flank scales are shown in detail. **D, E,** LDM 260/9. **E,** unknown symmetrical element.

4.35. att. Bruņuzivs *Asterolepis ornata* mazuļa ar zvīņām klātā astes daļa. **A,** ar saglabājušos dorsālo peldspuru. LDM 260/80a, iekšskats (zvīņas ar tuberkulām ir ārskatā) (Upeniece, Upenieks, 1992, Pl.4, fig. 4). **B,** LDM 260/235a, iekšskats. Rāmītī fulkrālās zvīņas. **C,** LDM 260/88a, iekšskats. Rāmītī sānu zvīņas. **D, E,** LDM 260/9. **E,** nezināms simetrisks elements.

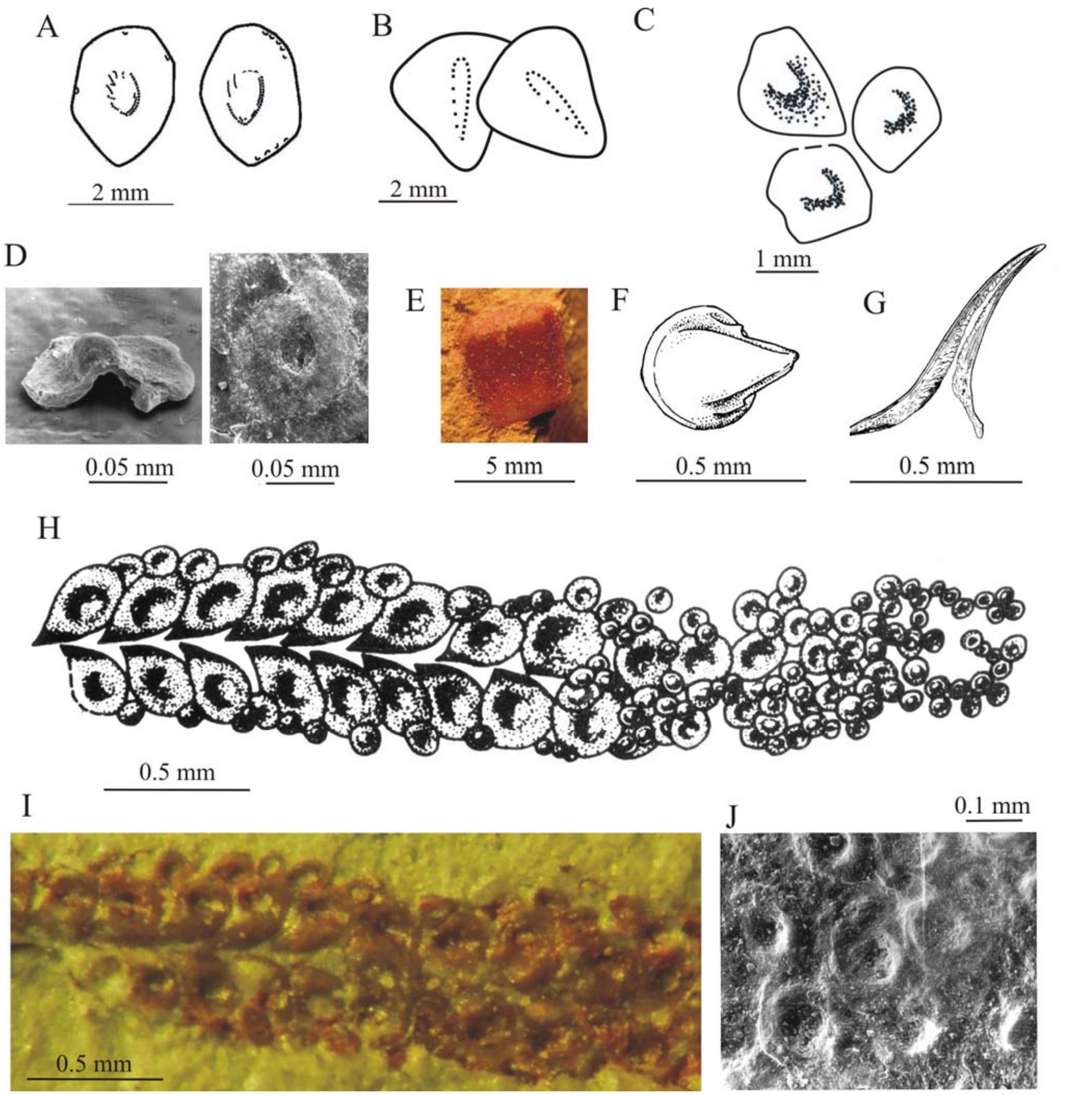


Fig. 4.36. Scales of some placoderm fish, (**A-E,H-J**) and of thelodonts (**F-G**). **A**, *Stensioella heintzi*, flank scale, in external view. Lower Devonian, Germany (Gross, 1962, fig. 6 B,G). **B**, *Pterichthyodes milleri*, flank scale, in external view. Middle Devonian, Scotland (Hemmings, 1978, Fig. 22 C). **C**, Yunnanolepididae, flank scale, in external and visceral views after Ivanov et al., 1996, Fig. 8 I, M. Lower Devonian, China (Wang, 1991, fragment of Pl.1 A). **D,E,H-J, *Asterolepis ornata,*** Upper Devonian, Latvia, Lode quarry. **D, H-J, of juvenile**. **D**, flank scales, in external and visceral views (Ivanov et al., 1996, Fig. 8 I, M). **H-I,** raw of fulcral scales in visceral view. **H,** with patch of flank scales in external view (on the right side), LDM 260/9 (Upeniece, Upenieks, 1992, fig.4). **I,** LDM 260/9. **J,** flank scales (Ivanov et al., 1996, Fig. 8 L). **E**, **scale of adult**, UP 10/1-5. **F, G,** scales of thelodont *Gampsolepis insueta.*

4.36. att. Dažu bruņuzivju (**A-E,H-J**) un telodontu (**F-G**) zvīņas. **A**, *Stensioella heintzi*, sānu zvīņa ārskatā. Apakšdevons, Vācija (Gross, 1962, fig. 6 B,G). **B**, *Pterichthyodes milleri*, sānu zvīņas ārskatā. Vidējais devons, Skotija (Hemmings, 1978, Fig. 22 C). **C**, Yunnanolepididae, sānu zvīņa ārskatā. Apakšdevons, Ķīna (Wang, 1991, fragment of Pl. 1 A). **D,E,H-J, *Asterolepis ornata,*** augšdevons, Latvija, Lodes karjers. **D, H-J, mazuļa astes zvīņas**, **D,** sānu zvīņas, ārskats un iekšskats (Ivanov et al., 1996, Fig. 8 I, M). **H-I,** kores zvīņas, iekšskats. **H**, pēc Upeniece, Upenieks, 1992, fig.4. **I**, LDM 260/9. **J**, sānu zvīņas, iekšskats (Ivanov et al., 1996, Fig. 8 L). **E**, **pieaugušas bruņuzivs zvīņa**, UP 10/1-5. **F,G,** telodonta *Gampsolepis insueta* zvīņas. Apakšdevons, Ukraina. **F**, ārskatā (Karatajūte-Talimaa, 1978, Pl. 48, fig.13) **G**, zvīņas plānslīpējums (ibid.: fig. 33-2).

The structure of the prominent inclined tubercle of the flank scales of *Asterolepis* juveniles resemble that (Fig. 4.36 A-C) of several Early and Middle Devonian adult placoderms (Upeniece, 2001): 1) the yunnanolepid antiarch *Liujiangolepis* from China, the oldest known articulated antiarch with associated scales (Wang S., 1987); 2) the tail fragment described as *Asterosteus* (Wang J., 1991; Ivanov *et al.*, 1996); 3) the scales of *Stensiöella* (Gross 1962: fig. 6 B, G); 4) as well as the scales of *Pterichthyodes* (Hemmings, 1978, fig. 22 C). Some resemblance in rather pointed although stout tubercles is seen in the squamation of the yunnanolepid antiarch from China *Parayunnanolepis xitunensis* (Fig. 4.37.). This type of the scale would be traced also in the Lower Devonian placoderm *Stensioella heintzi*, which exhibit a slightly similar median tubercle as well (Fig. 4.36.A), and possibly even within some agnathans, exhibiting resemblance in the shape of the inclined tubercle and the pulpar pit (Fig. 4.36. F,G).

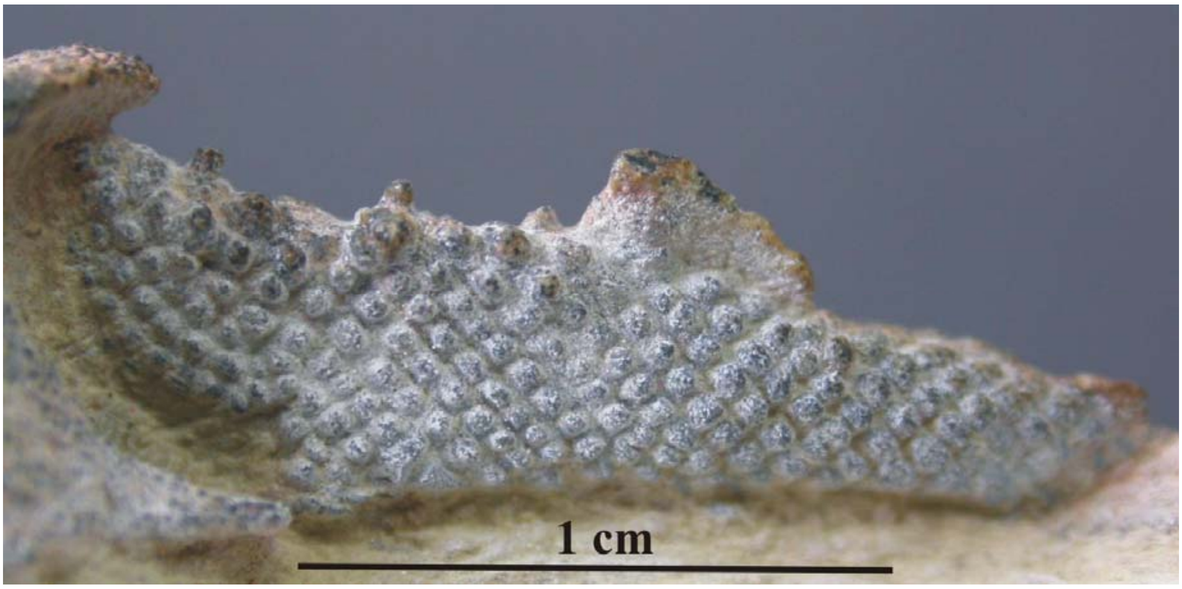


Fig. 4.37. The caudal part with dorsal fin of the small-sized yunnanolepid antiarch *Parayunnanolepis xitunensis*. Lower Devonian, China, Yunnan province. Specimen V 11679.1, housed in Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China.

4.37. att. Astes daļa ar dorsālo peldspuru sīka izmēra Yunnanolepididae bruņuzivij *Parayunnanolepis xitunensis*. Apakšdevons, Ķīna, Yunnan province. Paraugs V11679.1, Mugurkaulnieku paleontoloģijas un paleoantropoloģijas institūts Pekinā, Ķīna.

***Two types of scales*** can be clearly distinguished in juveniles: fulcral scales on the caudal crest and flank scales on the lateral and ventral walls. Both types of scales have a backward directed central tubercle on the outer surface and a corresponding pit on the inner surface. The tubercle and a pit on the scale disappear in adults, as mentioned previously.

***Flank scales*** are round and minute (Fig. 4.35 C). The base of a scale is circular, sometimes oval, its diameter reach 0.07 to 0.20 mm. The scales differ in size depending on the position and age of individual. Nevertheless very small ones with rather pronounced tubercles occurred sometimes between the large scales. Presumably during the growth of the squamation the appearance of additional new scales may take place. The scales on the ventral side are comparatively smaller than those on the lateral sides.

The diameter of a pit opening is variable. Overall, the pits on the scales of the smallest juveniles are comparatively larger than those of the advanced ones. The diameter of the pit comprises about a half of the scale base in the younger juveniles, and one/forth to one/fifth in the older ones. The pits start to gradually overgrown and hence the visceral surface of some scales appears smooth in the advanced juveniles (3rd ontogenetic stage, LDM 260/150). Some seldom preserved scales of the older known juvenile exhibit smooth visceral surface on the scales also (5th ontogenetic stage, LDM 260/10).

There are eight rows of flank scales on the lateral wall, as in adults (Ivanov *et al*., 1996, p. 405). The scales are located in longitudinal and in oblique rows. Flank scales usually are in contact or rarely slightly overlapped by the neighbouring row of scales. The non-overlapping position of the scale covering probably might have been caused by post-mortem circumstances.

There is a double row of ***fulcral scales*** behind the dorsal fin. There are two types of fulcral scales based on their shape and position on the caudal crest, as it is seen in adults of *Asterolepis*: roundish and elongated (Ivanov *et al*., 1996, figs. 1, 6 E, F). In juveniles the roundish ones represent a double row of about 4 pairs of large scales (diameter up to 0.35 mm in advanced individuals). Further a double row of elongated fulcral scales occurs: at least 44 pairs of scales (LDM 260/44), which bases are of a tapered elongated configuration (Figs. 4.35. B, detail; 4.36. H, I). Fulcral scales have also prominently inclined central tubercle (unknown for the adults), but their bases are larger than those of flank scales. These fulcral scales formed the dorsal caudal crest and have additional, dorsally and backward directed, elongated apices for the epichordal lobe of the caudal fin, as in adults (Ivanov *et al*., 1996, figs. 1, 6 F). The diameter of fulcral scale bases comprises about 0.25-0.30 mm. They are slightly overlapped, although non-overlapping areas are noticed. Fulcral scales of *Asterolepis* juveniles have some resemblance with these of adult of related antiarch *Pterichthyodes milleri* (Fig. 4.36. B, D).

Juvenile specimens bear visible dorsal and caudal fins (Fig. 4.35.). **Dorsal fin** lies not far from the posterior margin of the trunk shield: about in a distance of 1/9 of the total length of the caudal part and it can be seen only in several laterally compressed specimens. The dorsal fin is about 1.0-1.2 mm long and 0.3-0.7 mm high. There are three or four fulcral scales on the anterior margin of the dorsal fin. There are approximately four to five scale rows in the dorsal fin. Of these, the first consist of about 3-4 scales. The fourth consists of about 9-10 scales. **Caudal fin** is very slender (contrary to that in adults) and its tip consists of the diminishing row of elongated fulcral scales (Fig. 4.35. C).

### 4.1.10. Sensory canal system

Signs of the sensory line system visible on the fossil remains of juveniles of *Asterolepis ornata* appear in the relatively late stages of ontogeny. The middle pit-line groove (mpg) on the nuchal and paranuchal plates on the skull in one of the largest juvenile individual corresponding to the 4th stage of ontogenetic growth appear as the first evidence of the sensory line system (Fig. 4.46.). No other definite grooves for sensory lines can be observed on the head-shield and trunk armour plates of juveniles.

### 4.1.11. Ornamentation

Juveniles of *Asterolepis ornata* are represented by different stages of the development of the dermal armour, which are characterised by the strongly varying ornamentation (Figs. 4.38.; 4.39.). The ornamentation in juveniles differs considerably from that in subadult and adult individuals of *A.ornata,* the dermal bones of which generally are closely set with coarse and rounded tubercles (Fig. 4.40.). The ornamentation in subadults consists of small tubercles nearly equal in size (9-10 per 1 cm). In adults the tubercles are more low and less numerous (6-7 per 1 cm), besides several tubercles often are fused together. The most remarkable fusion occurred near the margins of the armour plates.

The ornamentation of dermal plates of juveniles in general consists of irregular network of anastomosing ridges and small meshes, unequal in size and outlines. During growth of the individuals, the ornamentation gradually underwent the following considerable transformations, which are listed here in accordance with the growth stages (growth stages are described below in chapter 4.2.3.):

1) Smooth surface without ornament characterises bones of the smallest individuals. The initial development of fine-meshed network took place along the ridge system, the rest area of the dermal armour plate is smooth (Figs. 4.5.; 4.25. B; 4.43.; 4.38. A). Smooth plates are typical for the 1st stage of growth (ontogeny).
2) Ornament of the fine-meshed network, which covers the most part of the armour plate, except the margins of the plate, where ornament is smooth (Fig. 4.38. B). Partial fine-meshed ornamentation is attributed to the transition between the 1st and the 2nd stage of ontogeny.
3) Ornament of the fine-meshed network, which covers all the dermal plate (Fig. 4.38. C, D). Complete fine-meshed ornamentation is attributed to the 2nd stage of ontogeny.
4) Ornament, gradually transformed from the fine-meshed network to the reticular network (Fig. 4.38. E), is attributed to the transition between the 2nd and the 3rd stage of ontogeny.
5) Ornament of clearly developed reticular network (Fig. 4.38. F). In places reticular network of anastomosing ridges with elevations at their points of union is developed. The elevations points are small, rather high and sometimes spine-like. All these features are attributed to the 3rd stage of ontogeny.
6) Reticular ornament of radially anastomosing ridges (Fig. 4.39. A) is attributed to the 4th stage of ontogeny.
7) Tubercular ornament of radially arranged tubercles in the points of union of anastomosing ridges corresponds to the 5th stage of ontogeny, although it initially started to develop already in the 4th stage of ontogeny (Fig. 4.39. B). Two last different types of the ornament can be observed on the same individual simultaneously (Fig. 4.46.).

The fine-meshed and reticular ornamentation of the dermal armour appear to be fairly typical in juveniles. It is worth to note that different types of the ornament can be observed on the same individual simultaneously, e.g., fine-meshed, reticular and tubercular ornament on the AMD plate (Fig. 4.39. C) or, for example, densely developed tubercles near the ossification centre of the armour plates and reticular ornamentation around the margins of the armour plates.

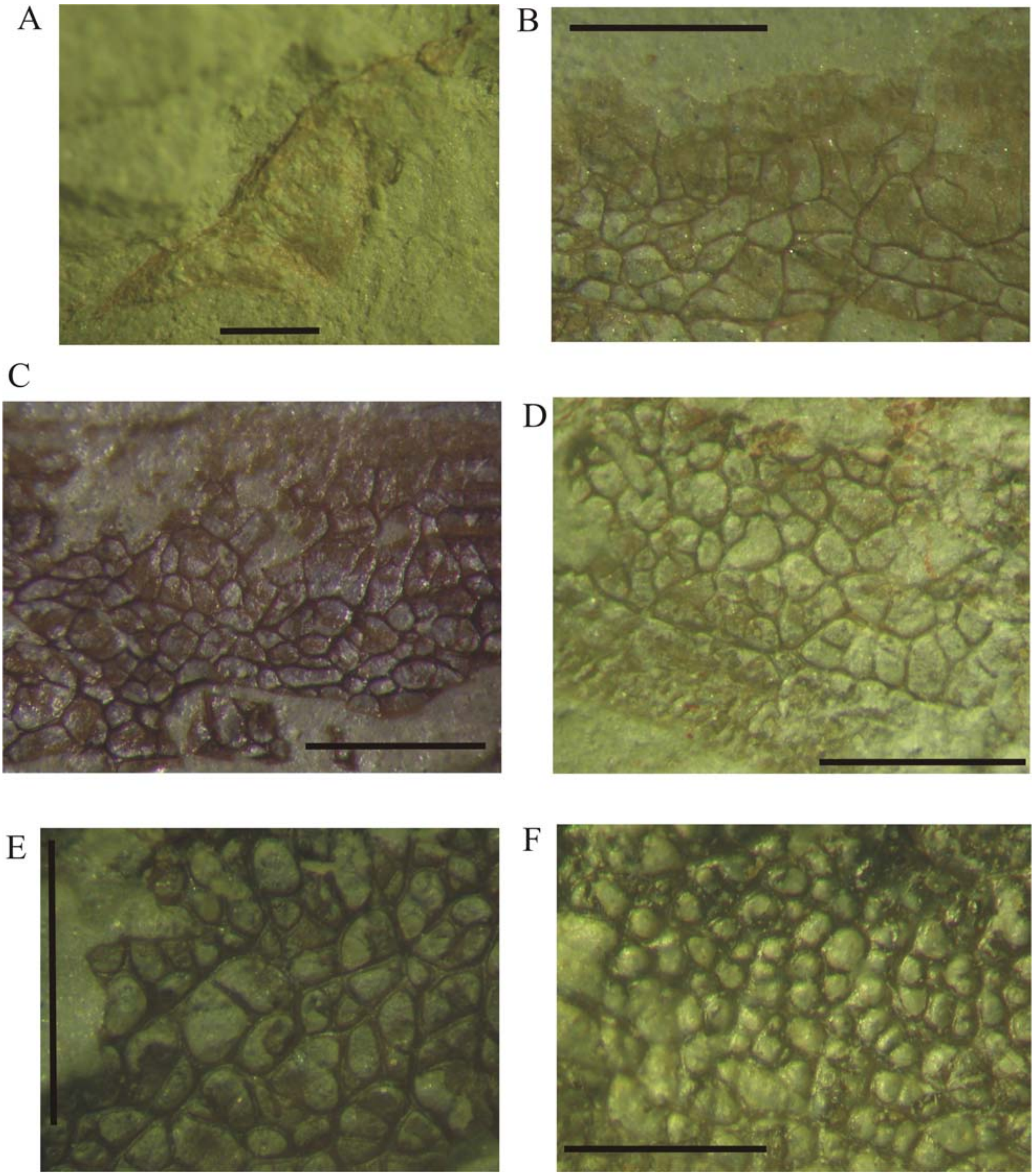


Fig. 4.38. Sequence of development of ornamentation of dermal bones in early growth stages in juveniles of *Asterolepis ornata.* **A**, Initial development of the fine-meshed network along the ridges of the ridge system. 1st ontogenetic stage. PVL plate LDM 260/500. **B**, Ornamentation of fine-meshed network covers the most area of the plate. Transition between the 1st and 2nd ontogenetic stage. AVL plate LDM 260/577. **C**, **D**, Fine-meshed ornamentation. 2nd ontogenetic stage. C, AVL plate LDM 260/489. D, ADL plate LDM 260/472. **E**, Transition between the 2nd and 3rd ontogenetic stage: fine-meshed ornamentation turns into the reticular one. AMD plate LDM 260/357. **F**, Reticular ornamentation. 3rd ontogenetic stage. PVL plate LDM 260/521. Scale bar 1 mm.

4.38. att. (iepr. lpp.) Dermālo kaulu ornamentējuma attīstības secība bruņuzivju *Asterolepis ornata* mazuļiem agrīnajās attīstības stadijās. **A**, Smalkā tīklojuma sākotnējā attīstība gar valnīšu sistēmas valnīšiem. Pirmā ontoģenētiskās attīstības stadija. PVL plātne LDM 260/500. **B**, Smalka tīklojuma ornamentējums klāj lielāko plātnes daļu. Starpstadija starp pirmo un otro ontoģenētiskās attīstības stadiju. AVL plātne LDM 260/577. **C**, **D**, Smalka tīklojuma ornamentējums. Otrā ontoģenētiskās attīstības stadija. C, AVL plātne LDM 260/489. D, ADL plātne LDM 260/472. **E**, Starpstadija starp otro un trešo ontoģenētiskās attīstības stadiju: smalka tīklojuma ornamentējums pārveidojas šūnveida ornamentējumā. AMD plātne LDM 260/357. **F**, Šūnveida ornamentējums. Trešā ontoģenētiskās attīstības stadija. PVL plātne LDM 260/521. Mēroga skala 1 mm.

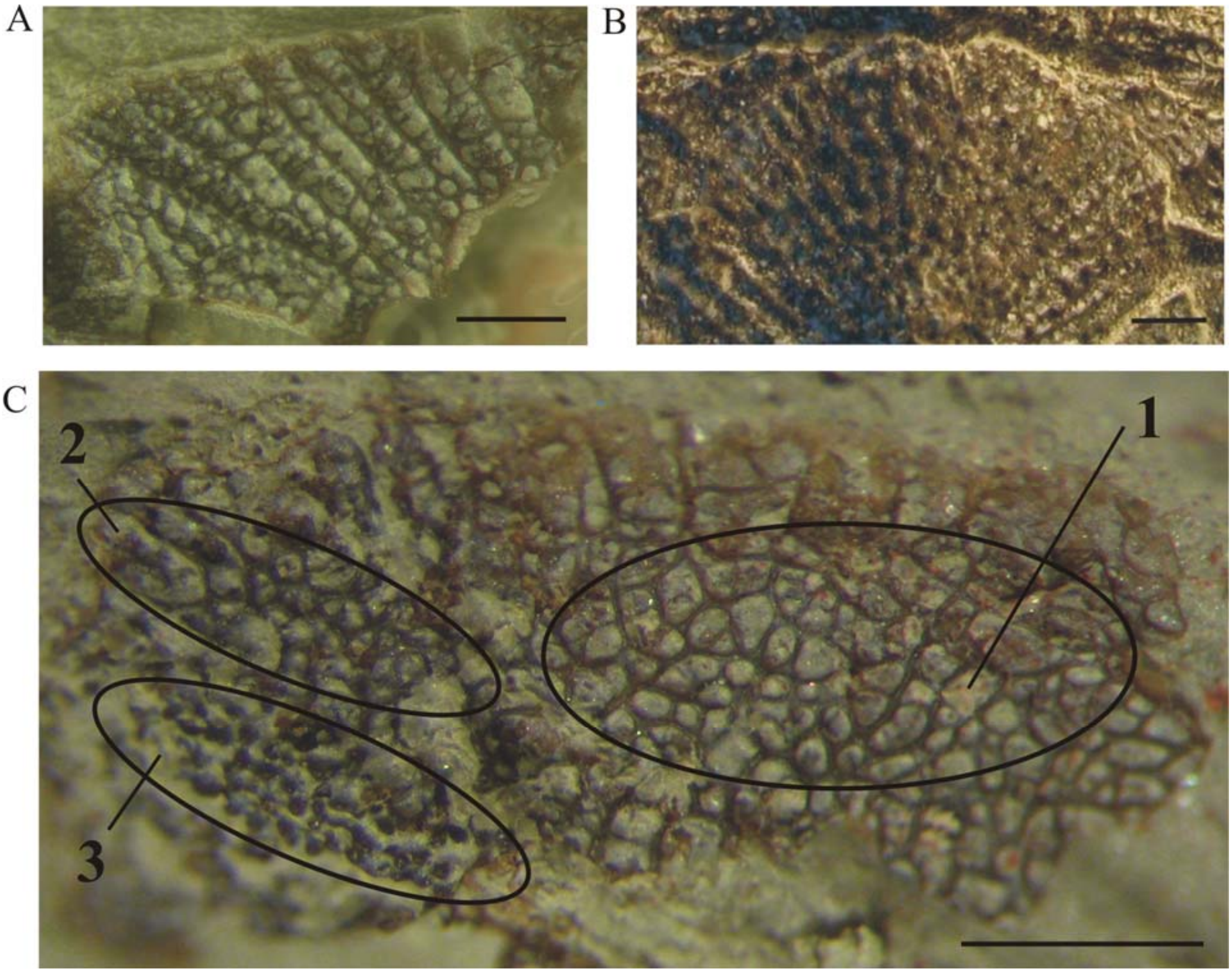


Fig. 4.39. Ornamentation of dermal bones in the advanced juveniles of *Asterolepis ornata*. **A**, Reticular ornament of radially anastomosing ridges. 4th ontogenetic stage. AMD plate LDM 260/539. **B**, Tubercular ornament of radially arranged tubercles in the points of union of anastomosing ridges. 5th ontogenetic stage. AMD plate LDM 260/78. **C**, Three types of ornamentation simultaneously presented on the plate: 1, fine-meshed, 2, reticular, 3, tubercular. AMD plate LDM 260/359. Scale bar 1 mm.

4.39. att. Dermālo kaulu ornamentējums lielākiem *Asterolepis ornata* bruņuzivju mazuļiem. **A**, Šūnveida ornamentējums ar radiāli savienotiem valnīšiem. Ceturtā ontoģenētiskās attīstības stadija. AMD plātne, LDM 260/539. **B**, Tuberkulārais ornamentējums ar radiāli izvietotām tuberkulām valnīšu krustpunktos. Piektā ontoģenētiskās attīstības stadija. AMD plātne, LDM 260/78. **C**, Vienlaicīgi esoši trīs ornamentējuma tipi uz bruņu plātnes: 1, smalks tīklojums, 2, šūnveida, 3, tuberkulārs. AMD plātne, LDM 260/359. Mēroga skala 1 mm.

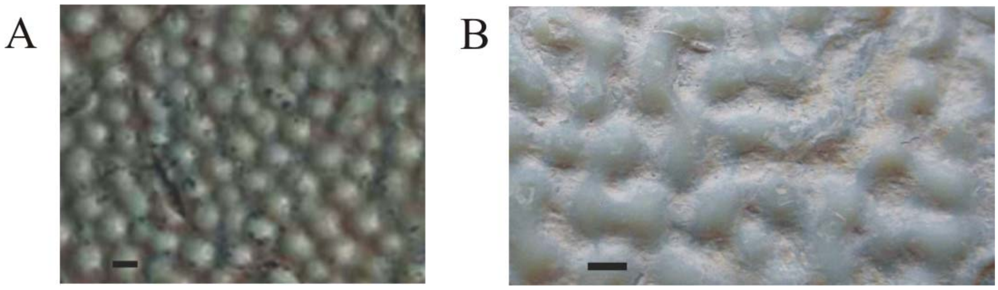


Fig. 4.40. Tubercular ornamentation of dermal bones of subadult (**A**) and adult (**B**) individuals of *Asterolepis ornata*. Scale bar 1 mm.

4.40. att. Dermālo kaulu tuberkulārs ornamentējums pusaugu (**A**) un pieaugušam (**B**) bruņuzivju *Asterolepis ornata* īpatnim. Mēroga skala 1 mm.

**Comparison of ornament of juveniles of *Asterolepis ornata* with that in some related antiarchs.** Some stages of the development of ornament in juveniles of *Asterolepis* exhibit similarity to the ornament in some related antiarchs as following.

Remarkably, that the smooth surface without the development of ornamentation is known in very small juveniles of *Bothriolepis canadensis* as well (Cloutier, 2010, Fig. 5A).

The ornament of the fine-meshed network of *Asterolepis ornata* juveniles characteristic for the 2nd ontogenetic stage is also seen in young individuals of related antiarch *Bothriolepis askini* from Antarctica (Young, 1988, fig. 19 A; Pl. 2, Figs. 1-7), and of *Bothriolepis canadensis* from Canada - pointed out by Stensiö (1948, p. 376), as well as marked on the AMD plate during studies by the author of the material in the Swedish Museum of Natural History in Stockholm (specimen is not numbered, it locates near the number P216). The ornament of the fine-meshed network is pointed out also for *B. cellulosa* (Stensiö, 1948, p. 423) and *B. prima* (Karatajūte-Talimaa, 1966, for MxL plate: Pl. 3, fig. 13; for AVL plate: Pl. 4, fig. 3).

The reticular ornament of *Asterolepis ornata* juveniles typical for the 3rd ontogenetic stage resembles that in the adults of the genus *Bothriolepis* (Stensiö, 1948), especially *Bothriolepis cellulosa* (Gross, 1941, Pl. 6, fig. 2), *B. prima* (Karatajūte-Talimaa, 1966, p. 198) and *B. obrutschewi* (*ibid*, Pl. 10, figs. 8, 9). Adult individuals of *B. obrutschewi* exhibit tubercular ornament (Karatajūte-Talimaa, 1966, p. 214), whereas small individuals show reticular ornament on the dorsal part (ibid, Pl. 10, Figs. 8, 9) and smooth surface on the ventral part (ibid, Pl. 9, Fig. 1b; Pl. 21, Fig. 3) of the trunk armour.

Similar reticular ornament is marked also on the PMD plate P 4249 (Swedish Museum of Natural History in Stockholm) of small individual of *Pterichthyodes milleri* from Scotland, observed by the author (Fig. 4.42. A,C). It was not described previously for *Pterichthyodes*. Hemmings (1978, p.38) has mentioned that small and adult individuals of *Pterichthyodes* exhibit tubercular ornament. Supposedly, juveniles of *Pterichthyodes* possessed a reticular ornament similarly to what is observed on juveniles of *Asterolepis* and *Bothriolepis*, as mentioned above.

The reticular ornament of radially anastomosing ridges typical for the 4th ontogenetic stage (Fig. 4.39. A) distributed on the central plates of the dorsal armour in juveniles of *Asterolepis ornata* resembles that in the adults of *Asterolepis radiata* (Karatajūte-Talimaa, 1963, fig. 48, Pl. XV).

Supposedly, that mentioned related antiarchs might have had a similar pattern for sequence of the development of ornamentation transformed from the fine-meshed ornament into reticular, sometimes of radially arranged anastomosing ridges, and finally into tubercular ornament. The more advanced ornament was developed first on the dorsal surface. It was pointed out also for *B. obrutschewi*: adult individuals possess tubercular ornament on the dorsal side (Karatajute-Talimaa, 1966, p.214), lateral side exhibits small tubercles, and ventral side shows reticular ornament. Small individuals exhibit reticular ornament on the dorsal side and no ornament on the ventral side, as mentioned above.

### 4.1.12. Internal structures

More than 100 specimens of juvenile *Asterolepis ornata* show structures within the anterior part of the left side of the trunk shield (in majority under the left ADL plate). These structures are well visible from the dorsal, ventral or inner side due to the arched armour plates over them (Fig. 4.41.). These structures appear with such regularity in position and shape that they must represent some internal organs communicating with the exterior. They are elongated and oriented lengthwise the body, and are filled with coprolite- like material as is found as discrete coprolites in the same clay lens. Carbonaceous and detritus-like bone material occurs in several cases, as well as numerous grains of quartz. This suggests that these remains are fossilised stomach contents, with the stomach full of digested food matter at the time of death of the animal (Upeniece, Upenieks, 1992; Upeniece, 2001). The size of the preserved stomach content is variable and comprises the following: 1x1.6 mm; 1x4.5 mm; 1.5x1.8 mm; 1.5x2.0 mm; 1.5x2.2 mm; 1.8x3.0 mm; 2x3.0 mm; 2x3.5 mm. The ratio length of the body armour to the length of the stomach content ranges from 4.3 up to 6.7.

In several cases such stomach contents with brown powdery mass, but of smaller size, were found also under the right ADL. It possibly could be explained as the result of displacement of the stomach content during the compaction of sediments. In few cases, the spots of similar powdery mass occur under the AMD plate also.

The fossilised remains of the last meal of fish, as well as an oogonium of the charophyte *Trochiliscus* sp., which has been found in the stomach content, point to the mud grubber behaviour of the juvenile *Asterolepis*, as is known from the cololites - mud filling content of the intestine of *Bothriolepis* (Denison, 1941; McAllister, 1996).

A noteworthy fact is that young individual of a related placoderm, the antiarch *Pterichthyodes milleri* P 4249 (Swedish Museum of Natural History in Stockholm) from Scotland, observed by the author, possess the identically located 2.5 mm long structure under the left ADL (Fig. 4.42. A, B). Presumably it could represent the stomach content. The length of the incomplete ventral side (from the level of the processus brachialis till the end of the PVL) of the mentioned juvenile individual of *Pterichthyodes* comprises 24.6 mm. The juveniles of *Asterolepis ornata* with marked area of stomach content represent the earlier stage of the development with the length of the incomplete ventral side reaching up to 12.3 mm, if compare with the young of *Pterichthyodes milleri*.

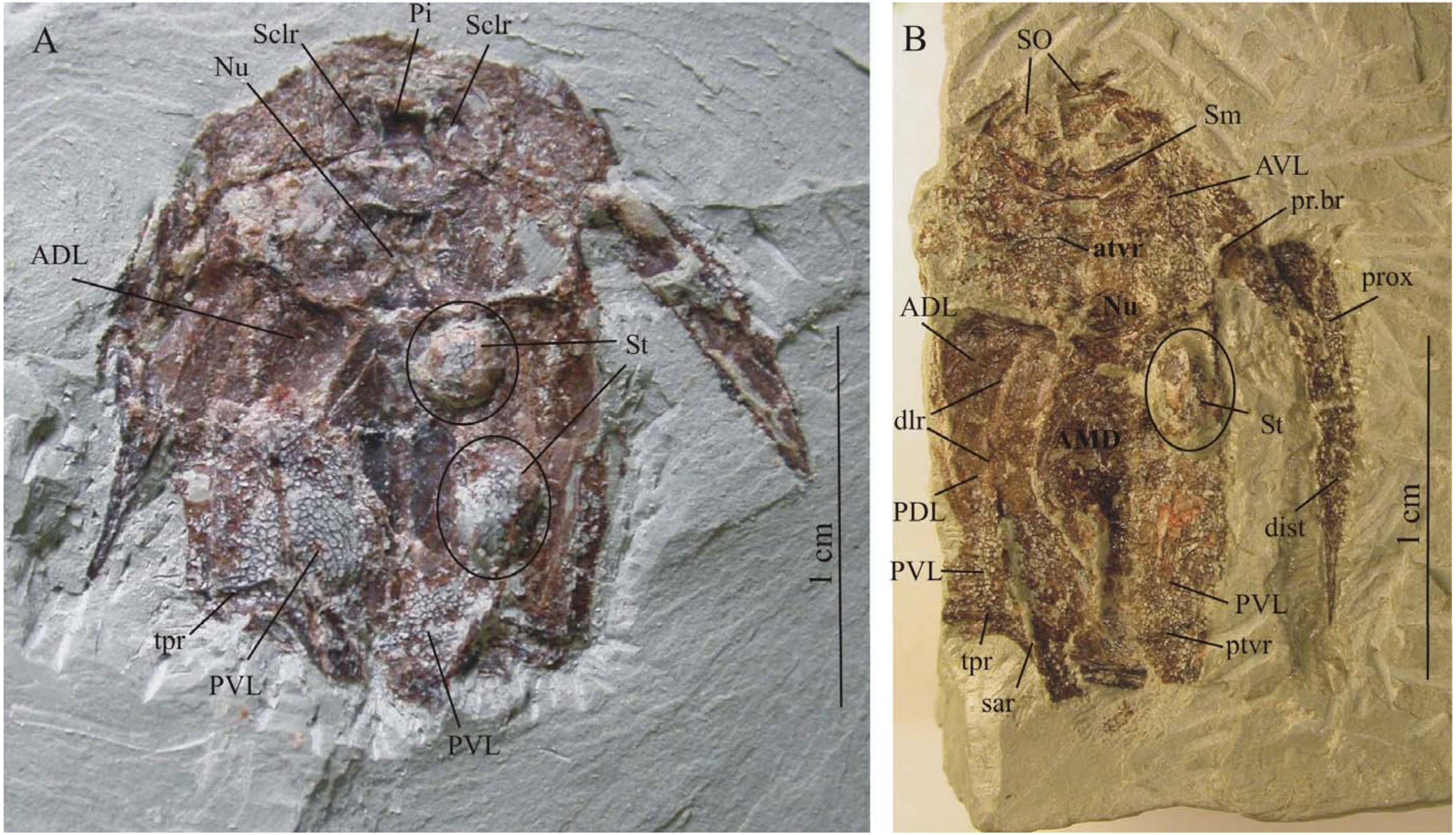


Fig. 4.41. Juvenile individuals of *Asterolepis ornata* with the preserved fossilised stomach content (St); ventral view (external view of some dorsal trunk armours` plates). **A,** LDM 260/260. **B,** LDM 260/1.

4.41. att. Bruņuzivju *Asterolepis ornata* mazuļi ar saglabājušos fosilizētu kuņģa saturu (St); ventrālais skats (dažas muguras bruņu plātnes ir ārskatā). **A,** LDM 260/260. **B,** LDM 260/1.

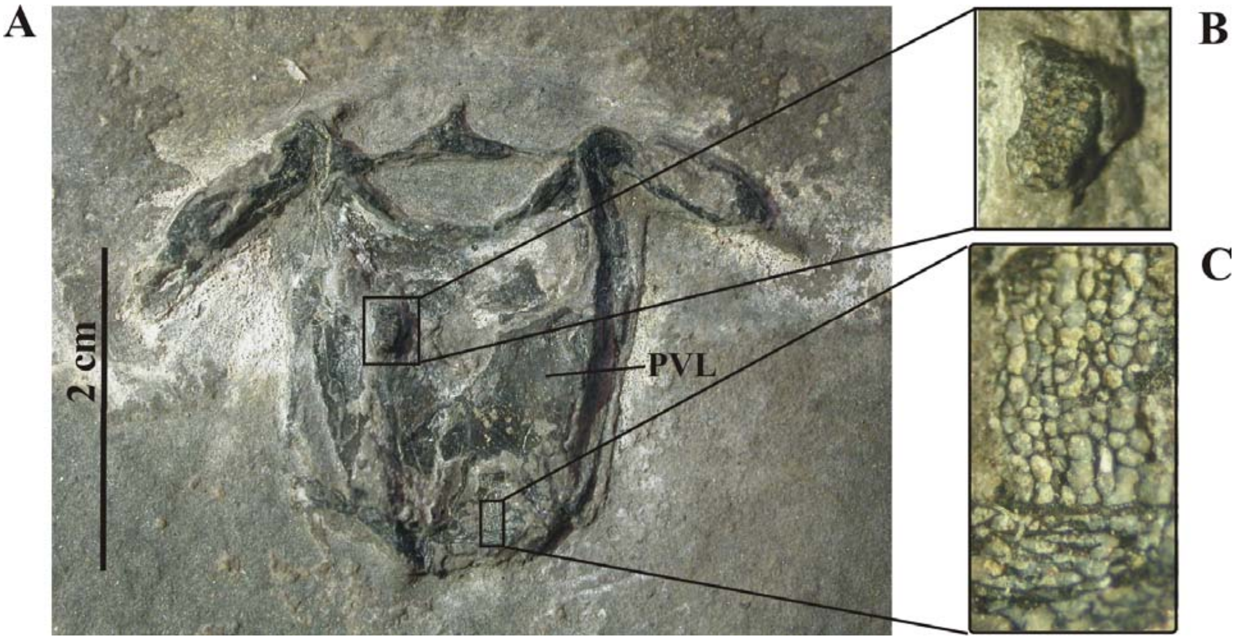


Fig. 4.42. Trunk armour of small individual of antiarch *Pterichthyodes milleri*; inside view of the ventral wall with parts (B,C) of external surface of the dorsal wall. Middle Devonian, Scotland. **A**, specimen P4249 (housed in Swedish Museum of Natural History, Stockholm). **B**, fossilised stomach content (beneath the left ADL plate). **C**, reticular ornamentation on PMD plate.

4.42. att. Bruņuzivs *Pterichthyodes milleri* neliela īpatņa rumpja bruņas; ventrālā sienas iekšskats ar detaļām (B,C) no dorsālās sienas, ārskats. Vidusdevons, Skotija. **A**, paraugs P4249 (Zviedrijas Dabas vēstures muzejā Stokholmā). **B**, fosilizēts kuņģa saturs (zem kreisās ADL plātnes). **C**, šūnveida ornamentējums uz PMD plātnes.

## 4.2. Changes of characters in *Asterolepis ornata* during the early growth

The sequence of the earliest growth stages has been established studying the development of the dermal armour of *Asterolepis ornata*. The total length of the dermal armour including head and trunk shieldsin juveniles is ranging from about 1.0 to 3.8 cm. For study purposes all *Asterolepis ornata* juvenile specimens were divided into five groups representing theoretical growth stages. Each of the growth (ontogenetic) stage is characterized by several morphological features, reflected the changes of the dermal armour. The small individual in the last, the fifth stage with an estimated length of the dermal armour 3.8 cm morphologically already resembles an adult form. Since the transition from one early growth stage to another was gradual, some individuals demonstrate the ’transitional stages’, representing mixture of features typical for the nearby stages. The majority of the recovered specimens (over 90%) corresponds to the second growth stage with the total length of the body armour about 1.5 cm, thus most probably representing mainly the remains of one particular shoal of young fishes.

There are also some separately found detached armour plates of ’adolescent’ individuals corresponding to the subadult growth stage. Subadult individuals are seldom observed at all, usually represented by isolated dermal armour plates. It is not a great shortage, because all visible morphological changes of the dermal armour and scale covering appeared already within the range of the earliest growth stages. So, the placoderm *Asterolepis ornata* now appears to be the well-known species by its` juvenile and adult representatives.

### 4.2.1. Morphological changes

Marked differences in morphology and shape peculiarities of young and adult individuals of *Asterolepis ornata* have been found. Juveniles differ from adults in the morphology of the caudal part (scales of juveniles have a tubercle on the dorsal surface), body proportions (the head occupies one third of the total body length etc.), in gradually changes of the ornament of the dermal armour during the early stages of ontogeny, in serratiform sutural connections, in absence of the medio ventral plate in the early stages of the ossification of the dermal armour, in uncovered area on the lateral wall, as well as in the presence of well developed ridge system (it diminishes in advanced juveniles). Some of the dermal plates of the trunk armour and of pectoral fins have been fused during the ontogeny: juveniles had separate PL and PDL plates instead of MxL plate. Unlike the adults, the juveniles had two dorsal and two ventral central plates, as well as an additional $Ml_5$ plate in the distal segment, as mentioned before.

**Transformations of shape of the body** are determined by the change of the proportions during the growth of the individual.

The changes in the shape of the head shield are marked by the changes of the shape of the orbital fenestra. It became relatively smaller with the growth, as mentioned before. Consequently the La plate became wider in its orbital part. The Pp plate exhibits considerably changes in proportions: it is short and wide in the smallest juveniles, later it gradually became longer and the contact area with the La plate remarkably enlarged. The shape of the Nu plate initially appeared almost roundish. Subsequently the remarkable depression for the Pp plate was developed along the anterior margin of the Nu plate during growth. Along the posterior part of the Nu plate the vertical posterior wall has formed. The Prm plate exhibits differences in the shape and proportions to compare with that in adults. The ridge system in advanced juveniles initially had been diminished from the central part of the head-shield. The bones, situated most laterally from the orbital fenestra, exhibit comparatively small changes in their shape (the Pn, Pmg, SM plates).

The changes in the shape of the trunk-armour are as following. The widest area of the dorsal wall is at the level of *processus brachialis*, in adults – at its` middle. The anterior margin and anterior part of the AMD plate in juveniles is considerably wider than that in adults. Besides that the AMD bears the oblique transverse ridge (otr), not preserved in adults.

The anterior part of the AVL plate exhibit considerable changes: the anterior mesial corner is remarkably protruded; the anterior lateral corners are sharp and more laterally situated than in adults. The breadth of the ventral laminae of the both AVL and PVL plates demonstrate considerably enlargement: the smallest individuals have the ventral fontanel on the ventral wall, gradually it decreased in size and subsequently the MV plate started to ossify. The shape of the semilunar plate also exhibit changes: in juveniles the plate is narrower at the level of the antero-lateral corners, besides that they are directed more forward contrary to that in adults. The lateral wall also exhibited the fontanel; which subsequently decreased during growth due to enlargment of the adjacent plates. The pectoral fins are longer than in adults.

**Special characters of immaturity:**

1. Remarkable and well developed ridge system in the dermal armour (Figs. 4.3.; 4.4.; 4.6.; 4.19.). The ridge system gradually diminishes in the advanced juveniles of *Asterolepis ornata*. In adults only weak traces of the main ridges on the trunk armour are preserved (dmr, dlr, vlr). The paired low oblique transverse ridge (otr), characteristic for juveniles of *Asterolepis,* is noted as characters of immaturity in small individuals of *Bothriolepis canadensis* (Stensiö, 1948, p. 104).
2. Remarkable differences in the body proportions during the growth of the dermal armour, listed in chapter 4.1.2.
3. Incompletely developed laminae of the trunk armour plates in the earliest growth stage (Figs. 4.20.; 4.23.A; 4.25. A; 4.27. A).
4. Gradual changes of ornament of the dermal armour during the growth of individual (Figs. 4.38.; 4.39.):

a) Three-layered bone structure not developed in smaller juveniles: only basal layer is present, therefore the plates have smooth outer surface.
b) The reticular ornament appears on the surface when the three-layered bone structure starts to develop.
c) Tubercular-radial ornament on the central plates on the dorsal trunk armour appears.
d) Advanced juvenile individual has the same tubercular ornament as in adult ones, but tubercles are considerably smaller.

5. Lateral fontanel on the lateral wall between ADL, AVL, PL and PVL plates is present in the smallest juveniles. It gradually disappears with enlarging of the adjacent plates.
6. Ventral fontanel on the ventral wall between AVL and PVL plates: there is no median ventral plate in smaller juveniles (Fig. 4.28. A). MV starts to ossify when the three-layered bone structure has been developed in the adjacent ventral plates (Fig. 4.28. B).
7. Separate PDL and PL plates characteristic for juveniles (Fig. 4.24. C-E) have been fused into the MxL plate in subadults and adults (Fig. 4.24. G-J).
8. Two separate central plates ($Cd_3$ and $Cd_4$) in the distal segment of the pectoral fin (Fig. 4.33. C); it is only one central plate in adults. In the subadult growth stage the second

central plate ($Cd_4$) fuses with the terminal plate, but no sutural connection is visible.

9. There is an additional $Ml_5$ plate in the distal segment in juveniles as well (Fig. 4.33. B). In adults it has been fused with the terminal plate.
10. Changes in the scale morphology: in juveniles scales bear one external tubercle on the dorsal surface, corresponding to a pit on the inner surface (Fig. 4.36. D). In adults the pit disappears and external surface is covered with an ornament consisting of roundish tubercles.
11. Sensory lines are not imprinted in juveniles. First sensory line initially appears on the nuchal plate in the advanced juveniles (Fig. 4.46.).
12. There are well-developed serratiform sutural connections between the head-shield plates in the endocranium region, as well as between the armour plates of the pectoral fin of juveniles (Figs. 4.30. A-E; 4.31.). There are only few weakly pronounced traces of serratiform connections left in adults (Fig. 4.30. F,G).

### 4.2.2. Ontogenetic development of exoskeleton

The sequence of ontogenetic stages of exoskeleton development provided possibility to evaluate previously unknown pattern of the early growth of antiarch placoderms. Five stages of early ontogeny are determined for premature fish *Asterolepis ornata*, based on such changeable and observable characters as the total length of the dermal armour, ornamentation and histological structure of the armour plates, presence of the ridge system, sensory lines, fontanels and MxL plate, as well as the appearance of scales (Table 4.3.).

All these characters have been grouped into two groups of qualitatively and quantitatively changeable characters. Qualitatively changing characters includes: 1) morphological features of the armour plates such as ornament, development of sutural connections, structural changes of the armour plates (the 3-layered bone, ridge system); 2) spreading of the armour plates and scale covering; 3) morphological changes of scales; 4) development of the sensory line grooves. Quantitatively changing characters are: 1) body length; 2) the ratios between body parts; 3) thickness of the armour plates.

Exoskeleton of *Asterolepis ornata* undergoes extreme morphological change during the early ontogeny. The series of figures illustrate the head and trunk armours typical for all the first five stages of growth. The description of only the first five developmental stages (ontogeny) is provided below because no complete specimens of *A. ornata* demonstrating the subadult stage have been found so far.

Table 4.3. Ontogenetic stages of the early development of the dermal armour of juveniles of *Asterolepis ornata*

4.3. tabula. Bruņuzivju *Asterolepis ornata* mazuļu dermālo bruņu plātņu agrīnās ontoģenētiskās attīstības stadijas

| **Stage of ontogeny** | Total length of the dermal armour, cm | Ornamentation of the armour plates | Structural changes of the dermal bone | Ridge system | Scales | Sensory system | Presence of the ventral fontanel/ MV plate | Presence of the lateral fontanel | Presence of the MxL plate |
|---|---|---|---|---|---|---|---|---|---|
| **1** | 1.1 | No ornamentation (smooth), but fine-meshed along ridges | Only basal layer developed | Strongly developed | Not ossified | Not observed | Large ventral fontanel, MV not developed | Yes | No |
| **2** | 1.4-1.6 | Irregular fine-meshed network | Basal layer and initial development of 3-layered bone | -“- | With a pit on the ventral surface, and corresponding tubercle on the dorsal side | Not observed | Ventral fontanel or initial development of MV | Yes or no | No |
| **3** | 1.8-2.3 | Reticular | 3-layered bone structure | -“- | No pits on the ventral surface | Not observed | Well developed MV plate | No | No |
| **4** | 2.6 (estim.) | Reticular ornament of radially anastomosing ridges; and tubercular | -“- | Remarkably reduced | Not known | Known on the Nu, Pn plates | -“- | No | Not known |
| **5** | 3.8 (estim.) | -“- | -“- | -“- | Smooth surface | -“- | -“- | No | Not known |
| **6 (subadult)** | Not known | Fine-tubercular | -“- | Weakly developed | Not known | Not known | -“- | No | Yes |
| **adult** | 25.0-35.0 | Tubercular | -“- | Weak traces of some trunk ridges | Rhomboidal or roundish shape, tubercular ornament | On the whole body | -“- | No | Yes |

## <u>Ontogenetic stage 1</u>

**Length** of the head shield plus trunk armour is 1,1 cm.

**Material**: two disarticulated specimens LDM 260/156 and 260/200 (Fig. 4.43.), and several detached armour plates (Nu, LDM 260/383b, Fig. 4.12. A,B; AVL, LDM 260/458, Fig. 4.25. A,B; PVL, LDM 260/501, Fig. 4.27. A; PDL, LDM 260/437a,b, Fig. 4.24. A).

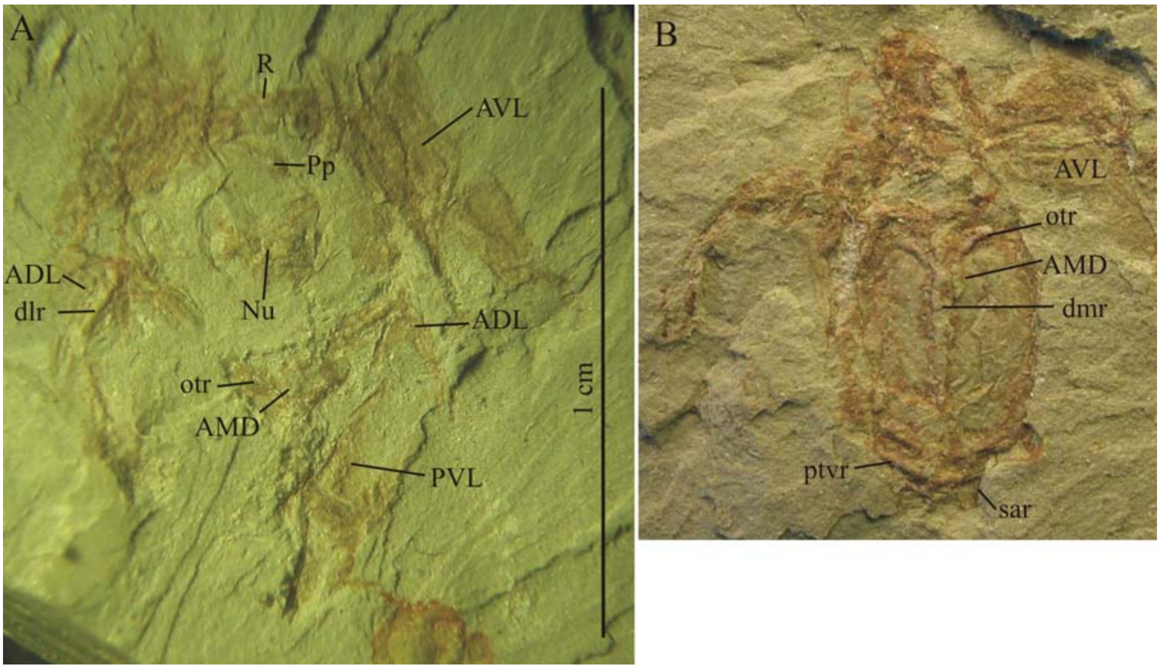


Fig. 4.43. The earliest known growth stages of juvenile individuals of *Asterolepis ornata*. The 1st stage of ontogeny. **A,** Disarticulated individual. LDM 260/200. **B,** Dorsal wall with detached AVL plate from the ventral wall. LDM 260/156. Upper Devonian, Liepa (Lode) pit, Latvia.

4.43. att. Paši mazākie atrastie bruņuzivju *Asterolepis ornata* mazuļi. Pirmais agrīnais dermālo bruņu plātņu attīstības posms (pirmā ontoģenētiskās attīstības stadija). **A,** Mazulis ar atdalītām bruņu plātnēm, LDM 260/200. **B,** Muguras bruņu plātnes ar atdalītu AVL plātni no ventrālās sienas, LDM 260/156. Augšdevons, Liepas (Lodes) mālu karjers, Latvija.

### Description

1. The dermal armour plates are very thin (0.0008-0.012 mm) and therefore translucent.
2. Mainly only basal bone layer is developed, therefore the plates have no ornament and are smooth. Weakly pronounced fine-meshed ornament occurs alongside the ridges of the ridge system of armour plates. In some places the second layer of the three-layered bone structure appears.
3. Laminae of the trunk armour plates are incompletely developed; plates do not overlap each other.
4. The ridge system consisting of a well pronounced ridges is developed on the head-shield and trunk armour (Figs. 4.5.; 4.43.).

5. Medio-ventral (MV) plate is absent on the ventral wall, the ventral fontanel is rather large.
6. The lateral fontanel between ADL and AVL is large and rhombic in shape (Figs. 4.19.; 4.20.).
7. The Nu plate has roundish shape (Fig. 4.12. A,B).
8. Scales are not ossified.

## Ontogenetic stage 2

**Length** of the head shield plus trunk armour is 1,4 to 1,6 cm.

**Material**: about 300 articulated and disarticulated individuals (over 90% of all found specimens), and a lot of detached armour plates (Figs. 4.1.; 4.2.; 4.9. A; 4.18.; 4.25. C,D; 4.28. A,B; 4.35. 4.44.).

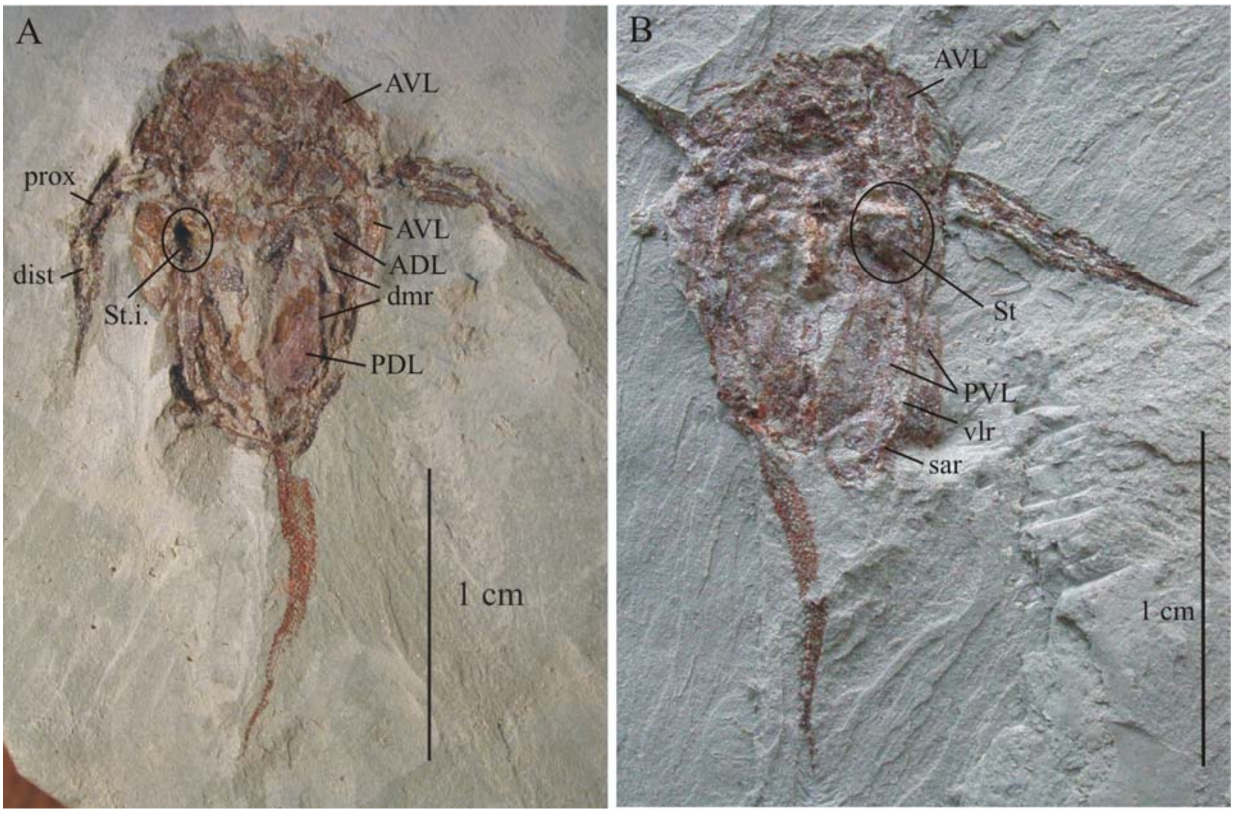


Fig. 4.44. Juvenile individuals of *Asterolepis ornata* with the well-preserved scale covering of the caudal part. The 2$^{nd}$ stage of ontogeny. **A,** Dorsal side. LDM 260/235b (Upeniece, 2001, Pl. 1, fig. 7). **B,** Ventral side. LDM 260/2a.

4.44. att. Bruņuzivju *Asterolepis ornata* mazuļi ar labi saglabājušos astes zvīņojumu. Otrais agrīnais dermālo bruņu plātņu attīstības posms (otrā ontoģenētiskās attīstības stadija). **A,** LDM 260/235b, dorsālais skats (Upeniece, 2001, Pl. 1, fig. 7). **B,** LDM 260/2, ventrālais skats.

### Description

1. The dermal armour plates are thin, but not translucent.
2. Plates show mainly three-layered bone structure, hence a well-pronounced ornament of irregular fine-meshed network appears (Fig. 4.38. C, D). The fine-meshed ornament develops at first on the dorsal side, only subsequently on the ventral side of individual.
3. Laminae of the trunk armour plates are completely developed.
4. The ridge system consisting of a well pronounced ridges is developed (Figs. 4.1.; 4.18.).
5. The MV plate is absent or present (Fig. 4.28. A,B); when present, only the basal layer of the bone is developed, therefore the MV plate appears as a translucent bone with smooth surface.
6. Indistinct overlapped areas are present on the trunk armour plates except the median bones of the dorsal trunk armour (AMD and PMD plates) (Figs. 4.21. A-C; 4.22. A).
7. The armour plates of the head shield and pectoral fin exhibit serratiform sutural connections with numerous, irregular and flat tubercles (Figs. 4.12 C,D; 4.30. A-E; 4.34. A-D).
8. Scales with a pit on the ventral side and corresponding tubercle on the dorsal side (Fig. 4.36. D).

## Ontogenetic stage 3

**Length** of the head shield plus trunk armour is 1,8 to 2,3 cm.

**Material**: several well-preserved articulated and disarticulated specimens (e.g., LDM 260/25a, 260/118a, 260/150a, 260/152a, 260/529), or disarticulated bones (PVL 260/152, PMD 260/529) (Figs. 4.9. B,C; 4.22. B; 4.23. E; 4.27. E; 4.42.; 4.45.).

### Description

1. The three-layered bone structure is well developed, with the well pronounced middle, spongious layer.
2. The well-pronounced reticular ornament is typical (Fig. 4.38. F), radially arranged tubercles occur on the central part of the Nu and AMD plates. More advanced ornament develops at first on the dorsal side of the individual, then it appears on the ventral side.
3. The MV plate bears reticular ornament.
4. Overlapped areas on the trunk armour plates are well pronounced.
5. The head shield plates exhibit serratiform sutural connections, tubercles are rare, denticular in appearance and roundish in the section (Fig. 4.12 E).
6. There are no pits on the ventral surface of the scales.
7. Pineal plate is rather arched (Fig. 4.9. C).

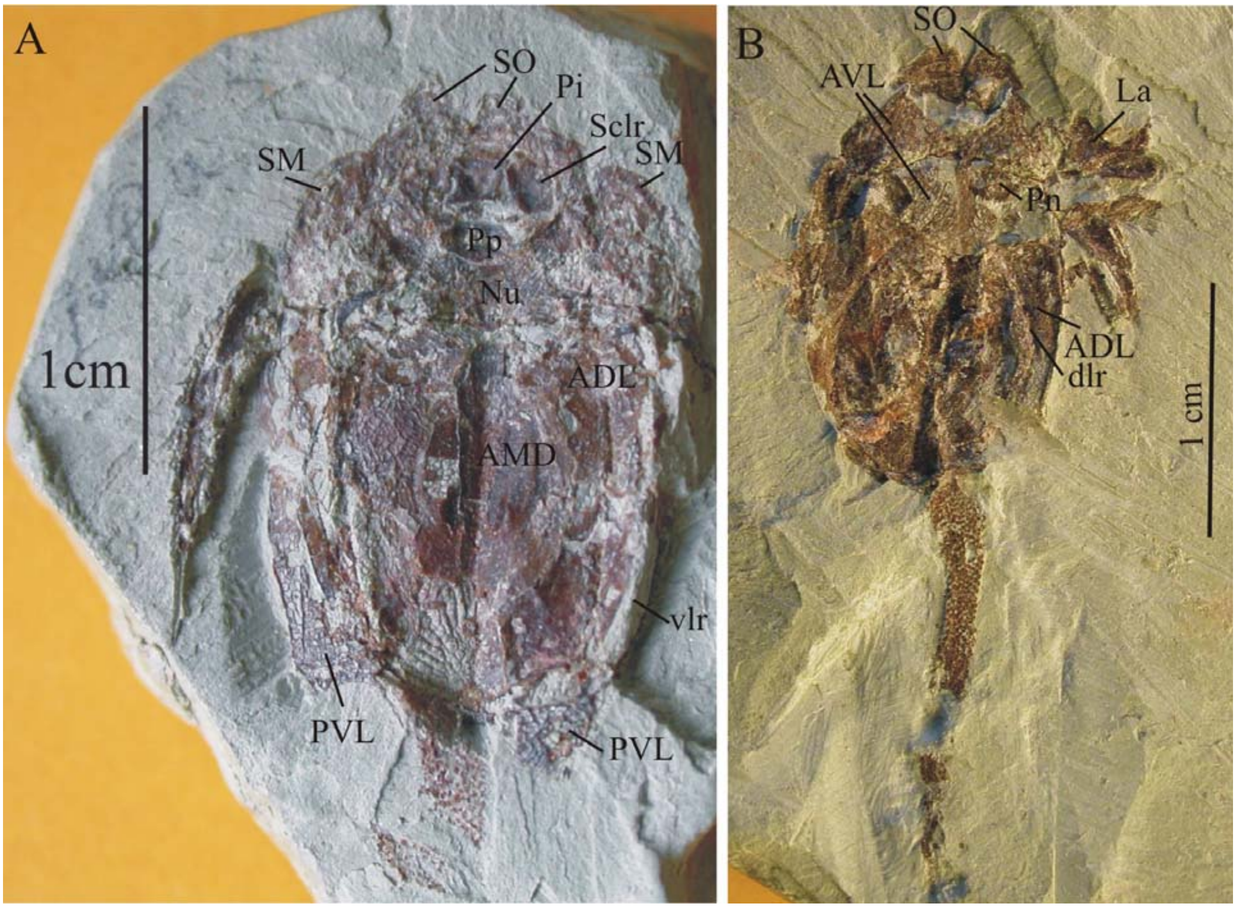


Fig. 4.45. Juvenile individuals of *Asterolepis ornata*. Ventral side. The 3rd stage of ontogeny. **A,** LDM 260/118a (Upeniece, 2001, Pl. 1, fig. 6). **B,** LDM 260/25a.

4.45. att. Bruņuzivju *Asterolepis ornata* mazuļi. Trešais agrīnais dermālo bruņu plātņu attīstības posms (trešā ontoģenētiskās attīstības stadija), ventrālais skats. **A,** LDM 260/118a (Upeniece, 2001, Pl. 1, fig. 6). **B,** LDM 260/25.

## Ontogenetic stage 4

Estimated **length** of the head shield plus trunk armour is 2,6 cm.

**Material**: one well preserved specimen consisting of the complete head shield and anterior part of the dorsal trunk armour LDM 260/78 (Figs. 4.9. E; 4.46.), one PMD plate LDM 260/529 (Fig. 4.22.B), as well as a fragment of the AMD plate LDM 260/539 (Fig. 4.39. A). No associated scales are known for this stage of ontogeny.

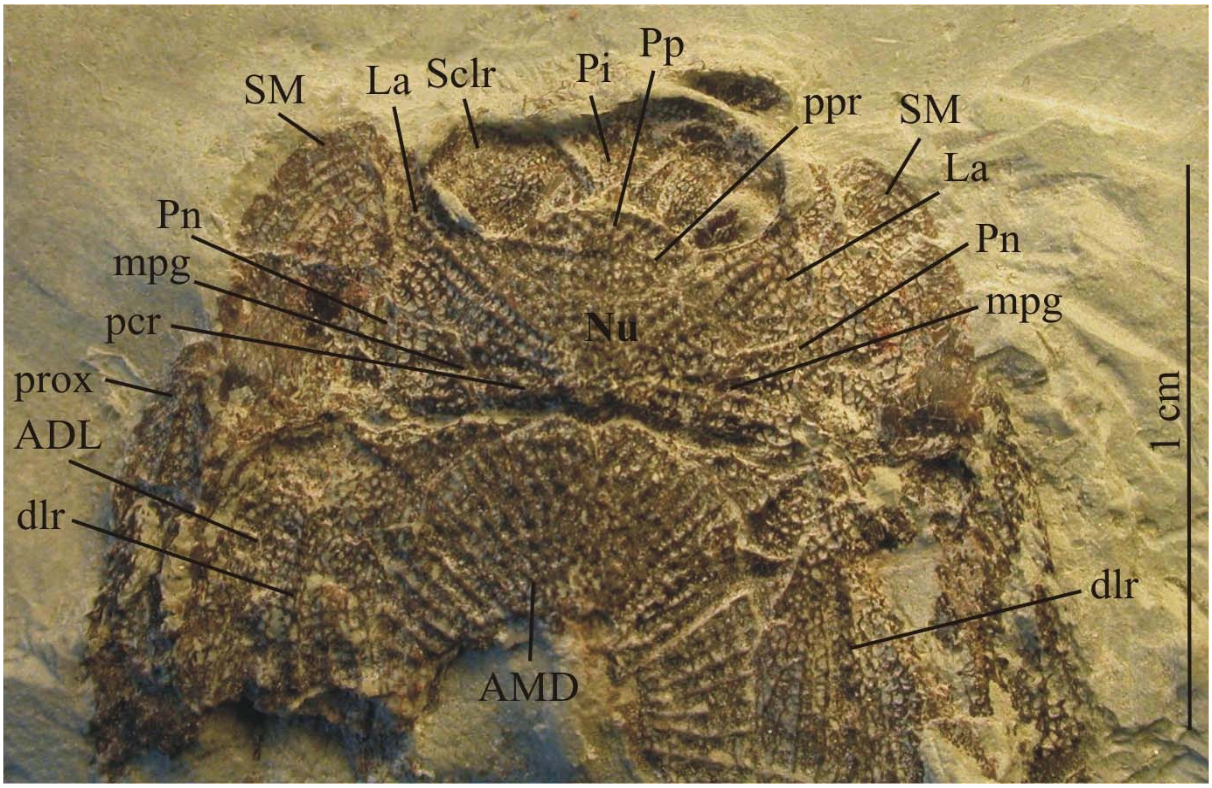


Fig. 4.46. Juvenile individual of *Asterolepis ornata*. The head-shield and anterior part of the dorsal trunk armour. The 4th stage of ontogeny. LDM 260/78.

4.46. att. Bruņuzivs *Asterolepis ornata* mazulis. Galvas vairoga bruņu plātnes un muguras priekšējā daļa. Ceturtais agrīnais dermālo bruņu plātņu attīstības posms (ceturtā ontoģenētiskās attīstības stadija). LDM 260/78.

### Description

1. The reticular ornament of radially anastomosing ridges is typical (Figs. 4.9. E; 4.39. A). The radially tuberculate ornament occurs on the central part of the Pp, Nu, AMD plates (Figs. 4.9.E; 4.39. B).
2. The ridge system on the head and trunk armour plates is remarkably reduced.
3. The pineal plate bears remarkably sharp and arched ridge, stretching with convexity along both lateral margins of the plate (Fig. 4.9. E).
4. Visible grooves of the sensory line system appear for the first time: the middle pit-line groove is seen on the Nu and Pn plates (Fig. 4.46.).

## Ontogenetic stage 5

Head-shield plus trunk armour 3.8 cm

**Length** of the head shield plus trunk armour is 3.8 cm.

**Material**: one incomplete articulated specimen LDM 260/10 (Fig. 4.47.) and one disarticulated AMD plate LDM 260/351 (Fig. 4.21. D).

Fig. 4.47. Incomplete juvenile individual of *Asterolepis ornata*. The 5th stage of ontogeny. Dorsal side. LDM 260/10.

4.47. att. Nepilnīgi saglabājies bruņuzivs *Asterolepis ornata* mazulis, dermālo bruņu plātņu piektā ontoģenētiskās attīstības stadija. Muguras puse. LDM 260/10.

**Description**

1. The ornament is tubercular along the central axis of the head and trunk covering such plates as Pp, Nu, and AMD, and reticular consisting of radially arranged anastomosing ridges along the lateral margins of Nu, La, ADL, and PDL plates.
2. The ridge system almost disappears.
3. The most advanced juvenile morphologically closely resemble the adult form.

## Development of the bone structure during the early ontogeny

The ornament of the dermal armour of *Asterolepis ornata* gradually changes during the early ontogeny as it was mentioned above, in the chapter 4.1.10. The sequence of the development of ornament is as following: smooth surface without ornament is changed into the smooth surface with initially developed fine-meshed network of weak ridges only along the ridges of the ridge system. Then the fine-meshed ornament covers the whole armour plate, gradually changing into the reticulate ornament and then into reticulate ornament with developed anastomosing ridges and elevations at their points of union. Reticular ornament with anastomosing ridges finally turns into the nearly tuberculate ornament typical for the most advanced juvenile individuals.

Two smallest tiny juvenile individuals (Fig. 4.43.) belonging to the 1st stage of ontogeny exhibit only translucent one-layered structure of the armour bones consisting of the basal layer. Respectively, armour plates are not ornamented at all (Upeniece, 2001b), demonstrating the smooth surface of the bone. The dermal plates consist of a thin compact 0.0008-0.012 mm thick bony lamina (Ivanov et al., 1995). Laminae of the trunk armour plates are incompletely developed; plates do not overlap each other.

A little larger juveniles in a transition stage between the ontogenetic stages 1 and 2 have smooth surface of the armour plates with initially developed fine-meshed network along the ridge system (Figs. 4.5.; 4.38. A).

A great majority of juvenile specimens represent the 2nd ontogenetic stage (Figs. 4.1.; 4.2.; 4.9. A; 4.18.; 4.28. A,B; 4.35. 4.44.). These juveniles have an ornament of a fine-meshed network consisting of the irregularly distributed bony trabeculae located on the external surface of the whole lamina except a narrow belt of initially weakly marked overlapping areas. The armour plates of the head shield and pectoral fin exhibit serratiform sutural connections with numerous, irregular and flat tubercles. Scarce vascular canals are opened on the outer surface of the plates. They are visible in the cross sections of the plate under trabeculae (Ivanov et al., 1995, Pl.1, fig. 1B).

It is typical that the more advanced ornament develops at first on the dorsal side: the fine-meshed network in this stage is well developed only on the dorsal wall, but initial development of the fine-meshed network is visible on the ventral side only along ridges of the ridge system, whereas the rest area is smooth.

The reticular ornament is characteristic for advanced juveniles (Figs. 4.42.; .4.45.) belonging to the ontogenetic stage 3. The three-layered structure of the armour plates is visible in juveniles in this ontogeny stage. It is composed of the three layers: basal, spongious and trabecular, similar as in adult individuals (Gross, 1931, fig. 1). The serratiform sutural connections of the head shield and pectoral fin become denticular in appearance and roundish in the section. Overlapping areas of the armour plates are well developed and well marked.

The same developmental pattern can be observed in this stage: more advanced ornament develops at first on the dorsal side: the same specimens show the reticulate ornament on the dorsal side, while the fine-meshed network covers plates of the ventral side of the armour. Such type of ornamentation is known for adults of *Bothriolepis* (Stensio, 1948; Young, 1988, Lukševičs, 2001a).

In larger juveniles in ontogenetic stage 4 (Fig. 4.46.) radially arranged ridges of reticulate ornament appear, e.g. on the AMD and ADL, as well as on the head shield (Figs. 4.9. E; 4.39. B). Then the radial ornamentation gradually disappears, except along the outer margins of the armour plates: somewhat suggestive to what is seen in adults of *Asterolepis radiata* (Karatajute-Talimaa, 1963, Pl. XIV, figs. 3,4; Pl. XV), as mentioned previously. Initial development of the radially tuberculate ornament is noticed in the central regions of the AMD and Nu plates of the same specimen.

In the largest juvenile individual in 5th stage of ontogeny (Fig. 4.47.) the radially arranged ridges are less marked, but tubercles became larger in diameter and flatter, similar to these of subadult (Fig. 4.40 A) individuals. In this stage, the juvenile already morphologically resemble an adult individual. In adults of *Asterolepis ornata* the ornament consists of irregularly situated coarse tubercles (Fig. 4.40. B).

Two major features can be distinguished for the developmental pattern of the ornament:

1. Ossification develops faster along the head-shield and trunk ridges therefore the more derived ornament is seen on and alongside the ridges, while the rest area of the armour plate is covered by the ornamentation typical for the respective developmental stage.
2. More advanced ornament develops first on the dorsal side of the head and trunk armour. The most complicated ornament can be observed on the posterior part of the head and on the median dorsal trunk plates, whereas it is least developed on the central part of the ventral wall of juveniles, e.g. in the MV and along the adjacent margins of the AVL and PVL plates (Upeniece, Upenieks, 1992, p. 173).

**Other known small-sized antiarchs.** There are several records of incompletely preserved small-sized antiarch placoderm individuals in the Devonian. Most of them are representing the more advanced ontogenetic stage of the dermal armour to compare with *Asterolepis ornata* juveniles, as well as they all have no preserved body squamation:

1. Recently found young individuals of *Bothriolepis canadensis* from Canada exhibit the minimum observed dorsal length of the whole armour (head shield plus trunk armour) of 0.6 cm (Cloutier, 2010, fig. 5A). Stensio (1948, p.229) reported on *B.canadensis* juveniles of 2.17 cm in total armour length; the amounted total length of the body in the smallest individuals is about 5.5 cm.

2. A very small specimen of *Bothriolepis* sp. from Mt Howitt, Victoria, Australia (Museum of Victoria) with an armour length of 1.8 cm shows also the very thin dermal armour (Werdelin, Long, 1986).

3. Several separate small armour plates of juveniles of *Bothriolepis askinae* from Antarctica (Young, 1988). The smallest dermal armour plates of detached juveniles of *Bothriolepis askinae* from Antarctica (Young, 1988) are little larger than respective armour plates in juveniles of *Asterolepis ornata*. The length of the smallest plates of *Asterolepis ornata*: AMD - 4.5 mm, PMD - 2.4 mm, ADL - 3.05 mm, PDL - 4.15 mm, AVL - 5.5 mm, PVL - 4.35 mm, Nu - 2.1 mm, La - 2.0 mm. The length of the smallest plates of *Bothriolepis askinae*: AMD – under 5 mm, PMD - 4.0 mm (ibid.: 43, 44). Marked changes of the shape of the ventral lamina of the AVL during growth are very similar in both taxa. (ibid.: fig. 23 C, D). Such changes in *Asterolepis ornata* occur in smaller juveniles (the length of the AVL plate 5.5 mm) than in *Bothriolepis askinae* (~10 mm, respectively). This might imply faster ontogeny in asterolepids.

4. Some small more or less completely preserved skeletons of juvenile individuals of *Bothriolepis panderi* from Russia (Lukševičs, Ivanov, 2006). The dorsal length of the head and trunk shield of the smallest complete specimen reaches 21 mm, but estimated dorsal length of the armour of partial specimen is 19 mm.

5. The finds of two hundred articulated juvenile individuals of *Bothriolepis* sp. from Upper Devonian Catskill Formation, Pennsylvania, USA were preliminary reported in Criswell et all. (2007). Most of the juveniles have a combined head and trunk shield length 30-35 mm. Little smaller specimens of them (head+trunk shield length in average 28 mm) are reported in Downs et al. (in press).

6. Internal mold of one partly articulated juvenile specimen of *Chuchinolepis gracilis* (Zhu, 1996, Fig. 20 A; Pl. VIII, Fig. 1). The estimated length of head + trunk armour is about 15.5 mm.

7. Other known small-sized antiarchs are Yunnanolepiform-like adult small-sized antiarch of *Minicrania lirouyii* from China (Zhu, Janvier, 1996). The tiny antiarch *Minicrania* (Yunnan, China) is preserved as internal and external molds (without any trace of bone); they are representatives of adult individuals. The smallest skull-roof in supposedly juvenile individual is less than 2.2 mm in length; the entire dermal armour in the presumed adult is less than 20 mm in length.

### 4.3. Discussion

A number of peculiar characters have been marked during the studies of the morphology of juvenile individuals of *Asterolepis ornata*. Many juvenile characters of *A. ornata* listed below have similarities to these in adults of other antiarch placoderms, but not to adults of *A. ornata*. Presumably, several of them would exhibit some degree of phylogenetical relationships within antiarchs. Changes of juvenile characters of *A. ornata* during the early ontogeny would reflect (more or less) the phylogeny of antiarch placoderms.

**1. Squamation**. *Asterolepis* juveniles exhibit morphologically different flank scales on the caudal part. The scales of juvenile individuals bear a prominent tubercle on the dorsal surface, corresponding to a pit on the visceral surface. Some resemblance in structure between the prominent tubercle of the flank scales of the caudal part of *Asterolepis* juveniles and those of some adult antiarch placoderms can be marked:

a) The tail fragment of the yunnanolepid described as Asterosteidae from the Lower Devonian, China (Wang J., 1991, Pl.1; mentioned in Ivanov *et al*., 1996).
b) The dorsal spinal scales of yunnanolepid antiarch *Liujiangolepis suni* (Wang S., 1987, p. 89) from the Lower Devonian, China. It is the oldest known articulated antiarch with associated scales.
c) The yunnanolepid antiarch *Parayunnanolepis xitunensis* from the Lower Devonian, China (Fig. 4.37.) (specimen figured in Zhang *et al*., 2001, Fig. 1A). Each flank scale exhibits a separate stout tubercle.
d) Flank scales of the Early Devonian asterolepidoid antiarch from Australia possess a median crest as well, but with markedly pointed end directed caudally (Young, 1984 b, fig. 8 A).
e) Flank scales of the Middle Devonian *Pterichthyodes milleri* (Fig. 4.36. B) possess a median crest. The above mentioned Early Devonian occurrences of separate tubercle on the each flank scale have more similarities with that of *Asterolepis* juveniles than those of Middle Devonian *Pterichthyodes*.
f) Fin scales of the Late Devonian *Bothriolepis gippslandiensis* exhibit small body denticles (Long, Werdelin, 1986, fig. 12 C).

This is the most ancient character that can be traced in the *Asterolepis* juveniles. This type of the scale would be traced also in the Lower Devonian placoderm *Stensioella heintzi*, which exhibit a slightly similar median tubercle as well (Fig. 4.36.A), and possibly even within some agnathans, exhibiting resemblance in the shape of the inclined tubercle and the pulpar pit (Fig. 4.36. F,G).

**2. Ridge system**. Well pronounced ridge system on the head and trunk armour in *Asterolepis* juveniles serves as a framework for strength for the very thin armour plates in juvenile stages (Figs. 4.4.; 4.6). In adults of *Asterolepis* the ridge system is nearly diminished, and only gentle remains of it as the dorso-median ridge (dmr) and ventro-lateral ridge (vlr) can be traced. Well-developed ridge system is known in a small-sized antiarch *Microbrachius* (dmr, dlr, otr, vlr, Hemmings, 1978, figs. 30.A, 31.B, 34.A, 36), and in adult tiny antiarch *Minicrania lirouyii* (dmr, dlr, otr, vlr, Zhu, Janvier, 1996, Figs. 4, 10 A,B). *Microbrachius* exhibit preserved transversal ridge near the posterior margin of the PMD plate (ptdr) also. Possibly, the anterior and posterior transverse ventral ridges (atvr, ptvr) are not preserved in *Microbrachius*.

*Minicrania* exhibit the weakly developed anterior and posterior transverse ventral ridges (atvr, ptvr) (Zhu, Janvier, 1996, Fig. 10), but there are no preserved transversal ridge near the posterior margin of the PMD plate (ptdr) and the posterior transverse lateral ridge on the lateral wall (ptlr). On the head-shield the *pcr* and *tcr* can be traced (*ibid*.: Fig. 4), as well as the well developed ridges around the orbital fenestra. *Minicrania* exhibit also some ridges, which are not marked in juveniles of *Asterolepis*. These are the medial dorso-lateral ridge (mr), and the transversal ridge on the lateral wall (*ibid*.: Fig. 11).

Other antiarchs, for example, *Pterichthyodes* exhibit only preserved dorsal and ventral trunk armour ridges (dmr, dlr, vlr, Hemmings, 1978, Figs. 9A, 10A, 11A, 13A, 15E). In *Bothriolepis* the dorso-medial ridge (dmr) sometimes forms the well developed large sized crest (*B. gippslandiensis, B. cullodenensis* in Long, Werdelin, 1986, Figs. 12, 16). The presence of the ridges in such primitive antiarch as *Minicrania* points that the well pronounced ridge system in *Asterolepis* juveniles must be referred to the most ancient characters of the Lower Devonian antiarchs.

**3. Ventral fontanel**. The absence of the median ventral plate (MV) in the smallest *Asterolepis* juveniles is similar to what is known in juvenile individuals of *Bothriolepis* sp. (Criswell et al., 2007; Downs et al., in press).

Several Early and Middle Devonian adult sinolepid antiarchs from China and Australia exhibit no presence of the MV plate (Ritchie *et al*., 1992): *Grenfellaspis, Dayaoshania* and *Xichonolepis*. The area of the ventral fontanel in the mentioned species belonging to the family Sinolepidae is remarkably large. Possibly the MV plate had not developed there at all and fontanel was covered only by the skin.

The MV plate was developed in juveniles of *Asterolepis* as the last plate in the dermal trunk armour. The MV plate in other antiarchs exhibits different relative size. For example, the MV plate in *Heteroyunnanolepis* occupies the most part of the ventral wall (Zhu, 1996, Fig. 17B), but usually the relative size of the MV plate is remarkably smaller. In *Asperaspis* the ventral fontanel was overgrown by the adjacent AVL and PVL plates, without any traces of the MV plate (Panteleyev, 1993, Fig. 4C). Presumably, the MV plate in antiarchs has been developed in different stages of ontogeny or has not been developed at all.

**4. Fusion of separate plates**. Juvenile individuals of *Asterolepis ornata* exhibit several non-fused bones during the early growth, which are completely fused in adults. It was observed in the following cases.

**PDL, PL and MxL**. Juveniles demonstrate separate posterior dorsal lateral (PDL) and posterior lateral (PL) plate. These plates merge together forming the mixilateral plate (MxL) in adults of *Asterolepis ornata*. The fusion of the PDL and PL plates has not been observed in the largest known juveniles of *Asterolepis*, hence this process might has occurred in the stage of subadult individuals.

All other species of the Middle and Upper Devonian *Asterolepis* possess the MxL plate in adult stage as well. Peculiarly, that *Asterolepis säve-söderberghi* from the Middle Devonian exhibits the almost entirely formed MxL plate in its` posterior third, whereas in the anterior two thirds the PDL and PL are separated by a suture or by clear vestiges of a suture. The suture is better developed in the smaller plates than in the larger ones, and it tends to disappear during the growth (Stensiö, Säve-Söderbergh, 1938, p.15, fig. 6). Genus *Asterolepis* first appear in the Lower Devonian of Belarus (Mark-Kurik, 2000, p.320), but no information about the condition of the MxL plate is available.

All up today known Lower Devonian antiarchs have separate PDL and PL plates, whereas antiarchs from the Middle and Upper Devonian exhibit either separate PDL and PL plates, or united MxL plate. Most of the Middle Devonian antiarchs possess the MxL plate. Both mentioned characters are distributed almost equally in antiarchs from the Upper Devonian deposits.

The MxL plate of the Middle Devonian antiarch *Sherbonaspis* exhibit preserved suture between the PDL and PL plates, and suture coincides with the lateral line groove (Young, Gorter, 1981, p.105). The suture and groove are also coincident in *Gerdalepis* (Gross, 1965, fig. 2). Hence, the lateral line groove of antiarchs possessing the MxL plate presumably would indicate the previous suture between the merged plates.

Obviously, the ancestor of *Asterolepis* possessed separate PDL and PL plates. The same condition in *Asterolepis* juveniles reflects phylogeny of antiarchs in the ontogeny of *A. ornata*. The nearest relatives of *Asterolepis*, namely *Pambulaspis* and *Remigolepis* exhibit separate PDL and PL plates as well.

Separate PDL and PL plates are known in adults of the Upper Devonian *Remigolepis*, *Pambulaspis*, *Grenfellaspis, Ningxialepis,* of the Middle Devonian *Byssacanthus, Stegolepis, Grossaspis, Gerdalepis, Asperaspis, Nawagiaspis, Xichonolepis,* (?$D_1$–$D_2$) *Dayoshania,* of the Lower Devonian *Yunnanolepis*, *Parayunnanolepis, Heteroyunnanolepis, Chuchinolepis, Phymolepis, Luquanolepis, Liujiangolepis, Zhanjilepis, Minicrania*, *Mizia, Vukhuclepis, Vanchienolepis*, and of the Upper Silurian *Silurolepis.* Presumably, the PDL and PL plates fused together in some antiarch during the Middle Devonian or even somewhat earlier and it might have appeared independently in each genus. Therefore such feature developed in the genus *Asterolepis* comparatively late.

**Distal segment of pectoral fin**. The distal segment of the pectoral fin bears two central plates in juveniles of *Asterolepis* ($Cd_3$ and $Cd_4$, Fig. 4.31. A-C). Contrary to that in adults of *Asterolepis* there is only one central bone ($Cd_3$) in the distal segment (*ibid.*: D,E). Other described until now antiarchs exhibit two or three central plates in the distal segment.

Juveniles possess the additional lateral marginal plate 5 ($Ml_5$) in the distal segment as well, which has not been observed in adults of *Asterolepis*. In adults of *Asterolepis* the $Ml_5$ plate and $Cd_4$ plate fuse together with the terminal plate (T, Fig. 4.31. D,E). The fusion of these three bones in the terminal plate might have occurred in the subadult stage of *Asterolepis ornata*.

Peculiarly, that the number of dermal plates in the pectoral fin in juveniles of *Asterolepis* coincides well with that, for example, of Middle Devonian antiarch *Pterichthyodes* (Fig. 4.31. F) or *Byssacanthus* (Karatajūte-Talimaa, 1960) and not with that in adult of *Asterolepis ornata*. That could point to reflection of some characters of phylogeny of antiarchs in the ontogeny of *Asterolepis*. Presumably, the ancestor of *Asterolepis* might have possessed two central bones and $Ml_5$ in the distal segment. The fusion of these bones in one terminal plate might be took place only within the genus *Asterolepis*. The *Asterolepis* sp. from the Middle Devonian of Belgium exhibit separate $Cv_4$, $Ml_5$ in the distal segment of the pectoral fin (Gross, 1965, fig. 1G) as well. For the time being the genus *Asterolepis* is only one who exhibits the one central bone in the distal segment in the adult forms.

**5. Proportions of the body and plates**. Some proportions in *Asterolepis* juveniles exhibit similarities with these in adults of other antiarchs and not with that in adults of *Asterolepis*.

**Pectoral fin**. The length of the pectoral fins in *Asterolepis* juveniles exceeds the trunk armour similarly as in adults of *Bothriolepis* (Stensiö, 1948, fig. 116). In adults of *Asterolepis* the length of the pectoral fin comprises only two thirds of the trunk armour (Lyarskaya, 1981, fig. 74).

**AVL plate**. The lateral lamina of the AVL plate in juveniles (Figs. 4.25. A,B; 4.26. B) is highest across the *foramen axillaris*, and declines in its posterior part, similar to that in *Bothriolepis* (4.26. F). Contrary, in adults of *Asterolepis* the lateral lamina is highest in its posterior part (Fig. 4.26.D). Presumably, this explains why the trunk armour of *Asterolepis* is relatively larger than that in *Bothriolepis*.

**AMD plate**. A wide anterior margin of the AMD plate in *Asterolepis* juveniles is similar to that in adults of the Middle and Upper Devonian antiarch *Bothriolepis* (Pan, *et al.*, 1987, fig. 22; Stensiö, 1948, figs. 118, 121), Middle Devonian *Pterichthyodes* (Hemmings, 1978, fig. 9) and *Microbrachius* (Hemmings, 1978, fig. 36), and the Upper Devonian *Kirgisolepis* (Panteleyev, 1992, fig. 1A). Related genus *Pambulaspis* exhibits a slightly wider anterior margin of the AMD plate than adults of *Asterolepis*, and is more similar to that in *Bothriolepis*. Presumably, the ancestor of asterolepids and bothriolepids could possess the wide anterior margin of the AMD plate.

The Lower Devonian antiarchs (Yunnanolepididae) mostly possess the AMD plate with the pointed anterior margin (Zhu, M. 1996), except the *Liujiangolepis suni* (Wang S., 1987, fig.1). Possibly, the wide anterior margin of the AMD plate appeared during the Middle Devonian. The above mentioned characters of proportions may reflect some relations between the botriolepids and juveniles of *Asterolepis*.

6. **Ornamentation**. The changing ornamentations in *Asterolepis* juveniles during the growth can be compared with the patterns of changes of ornamentation of some other antiarchs. For example, the fine-meshed ornamentation typical for the 2nd stage of the development in *Asterolepis* juveniles resembles that in adults of *Bothriolepis portalensis* (Young, 1988, Pl. 10, figs. 5,6); the reticular ornamentation of the 3rd stage of the development resembles that in adults of *Bothriolepis prima, B. obrutschewi* (Karatajūte-Talimaa, 1966), etc.; the radially tuberculate ornamentation characteristic for the 4th and 5th stages of ontogeny resembles that in adults of *Asterolepis radiata* (Karatajūte-Talimaa, 1963, fig. 48).

The earliest known antiarchs (Yunnanolepididae) exhibit tubercular ornamentation, but Bothriolepididae mostly show the reticular ornamentation. Presumably, the reticular ornamentation emerged later. The similarities of the ornamentation between juveniles of *Asterolepis* and adults of *Bothriolepis* would point to that the ornamentation in the ancestor of *Asterolepis* was similar to that in bothriolepids. The development of the ornamentation in *Asterolepis ornata* juveniles during the growth could point that the ancestor of *Asterolepis* could have possessed the reticular ornamentation.

In conclusion it would be said that the juveniles of *Asterolepis* exhibit some bothriolepidoid characters, which are not observed in adults of *Asterolepis*. The ancestor of *Asterolepis* possibly might have possessed several the above mentioned bothriolepidoid characters. The *Asterolepis* and *Bothriolepis* might have a common ancestor with characters somewhat similar to the Middle Devonian antiarch *Dianolepis* (Chang, 1965, Pl. 2) and other Dianolepididae, which exhibit "mixture" of features typical both to *Asterolepis* and *Bothriolepis*.

# 5. Morphology and ontogeny of *Lodeacanthus gaujicus* Upeniece

## 5.1. Morphology of *Lodeacanthus gaujicus*

### 5.1.1. General remarks

Acanthodians are a fossil group of the earliest gnathostomes characterized by the presence of large spines in front of all fins except the caudal fin, and by the particular scale type with a bulging base. Since they are nektonic fishes, most acanthodians have wide distribution areas, therefore their scales and spines are successfully used for biostratigraphical purposes (Valiukevičius, 1994, 1995, 2003, 2005).

Acanthodians occur on all continents in rocks ranging from the Late Ordovician till the Early Permian, but they are a poorly known group due to the rarity of intact material. Their micromeric exoskeleton and poorly ossified endoskeleton make them rare as fossils even in good burial conditions (Denison, 1976; Janvier, 1996). The majority of taxa have been described from Scotland (Watson, 1937; Miles, 1973a), Canada (Bernacsek, Dineley, 1977; Gagnier, 1996), North America (Zidek, 1976), Germany (Miles, 1966), Russia (Novitskaya, Obruchev, 1964; Valiukevičius, 1992), Australia (Long, 1983, 1986), and Latvia (Upeniece, 1996, 2001b).

Acanthodians are relatively rare in the Gauja Regional Stage of the Main Devonian Field. They are represented by scales and fin spines of *Acanthoides?*, cf. *Cheiracanthus*, *Devononchus*, *Haplacanthus*, *Homacanthus*, *Diplacanthus*, *Rhadinacanthus*, *Nostolepis*, *Nodocosta* (Valiukevičius, 2000). Very peculiar and unique in the good preservation is representative of mesacanthids *Lodeacanthus gaujicus* Upeniece, 1996, which has been described based on the whole-bodied specimens from the Lode quarry. Specimens of *Lodeacanthus* were collected during the 1989-1999 field seasons by the author (Upeniece, 1991, 1993, 1996, 2001b, 2005b).

**A collection of *Lodeacanthus gaujicus*** contains over sixty whole-bodied, disarticulated and fragmentary preserved individuals ranging from about 0.8 to 4.8 cm in estimated total length. Specimens are preserved in all stages of growth: both juvenile and presumably adult or at least nearly mature individuals (with developed entire squamation) are present (Figs. 5.1, 5.2). This represents the only known sequence of the development of Devonian acanthodians up to now.

About one fourth of the specimens are clearly juveniles, judging from fish fry with an incomplete development of squamation or they demonstrate merely a film of the skin with fin spines and head elements, allowing the discernment of several aspects of its ontogenetic development (Upeniece, 2005b, 2011). The smallest larval - juvenile individual of *Lodeacanthus* (Fig. 5.2) comprises the smallest whole-bodied acanthodian described until now.

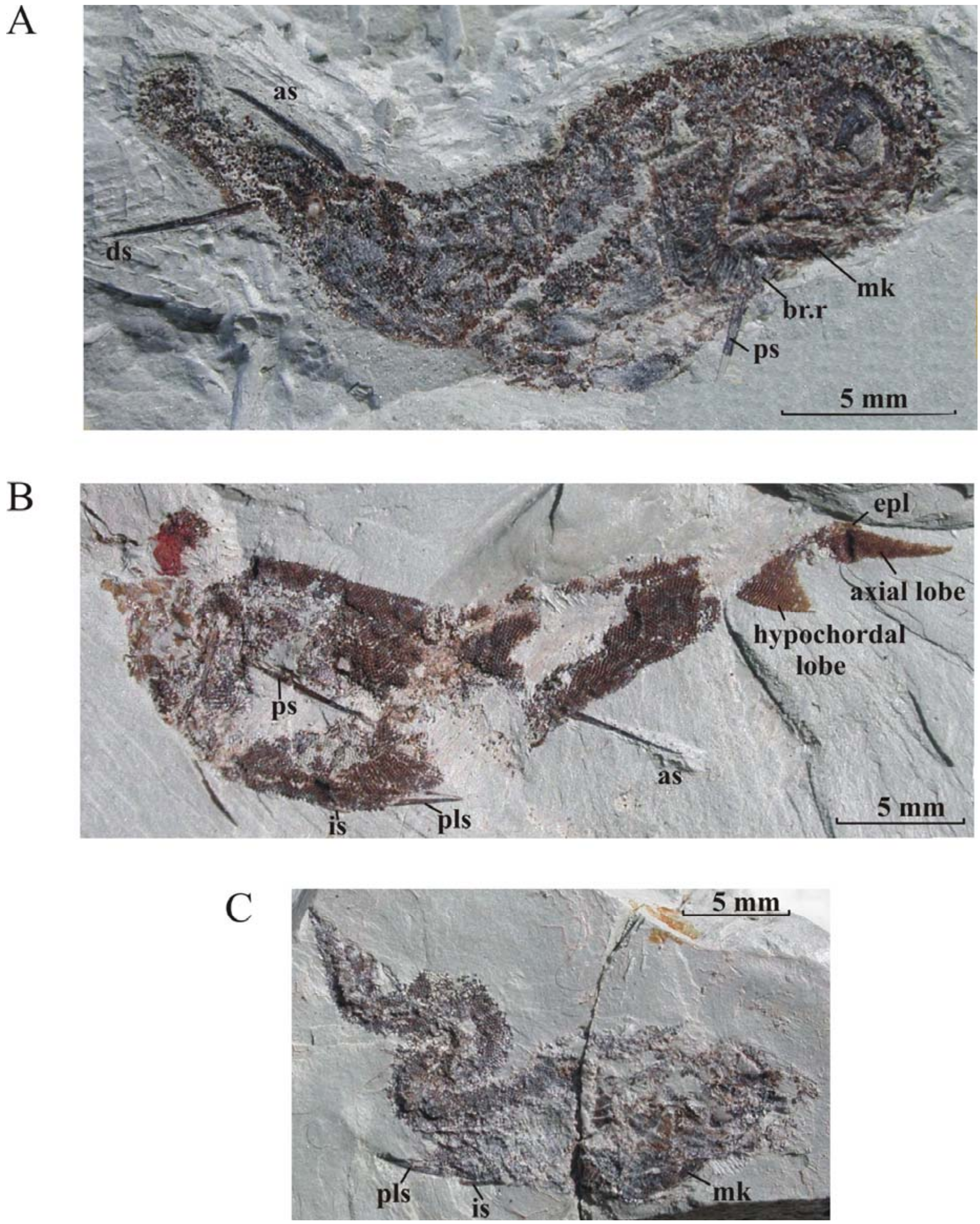


Fig. 5.1. Completely squamated (presumably adult) individuals of acanthodian *Lodeacanthus gaujicus* Upeniece. **A**, LDM 270/19a (caudal part turned over); **B**, LDM 270/9a; **C**, LDM 270/7a.

5.1. att. Veseli akantožu (domājams, pieaugušu īndivīdu) skeleti *Lodeacanthus gaujicus* Upeniece. **A**, LDM 270/19a; **B**, LDM 270/9a; **C**, LDM 270/7a.

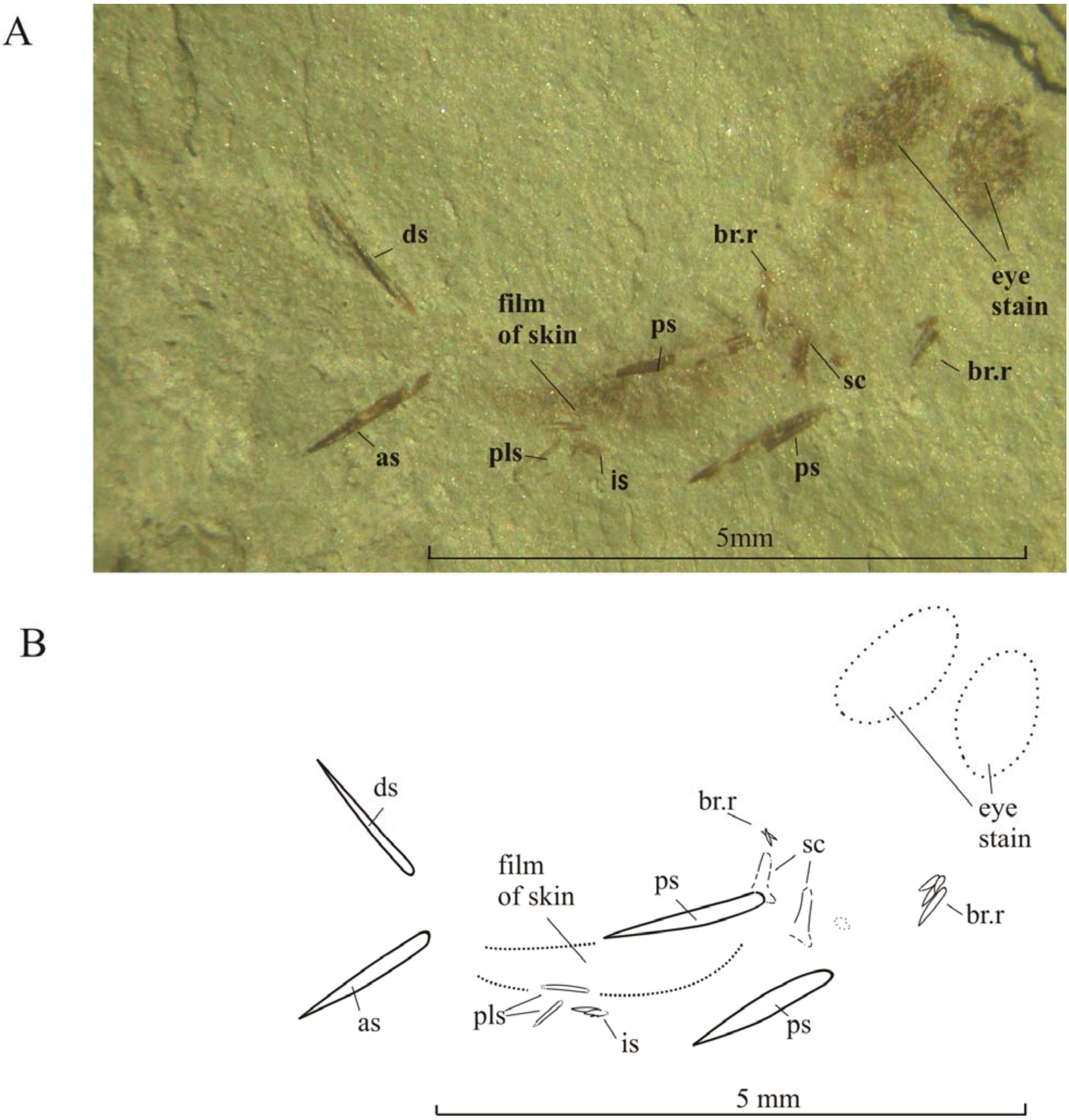


Fig. 5.2. The smallest known acanthodian larval-juvenile individual of *Lodeacanthus gaujicus* without the squamation. It represents the smallest described until now whole-bodied acanthodian. The body is covered merely with a film of skin, the head is indicated only by the presence of an eye stain, and a few branchiostegal rays. Well-developed fin spines and scapula indicate a presence of an acanthodian individual. **A**, photo of specimen LDM 270/45 a; **B**, drawing from a part and counterpart: LDM 270/45 a, LDM 270/45 b.

5.2. att. Mazākais zināmais akantodes *Lodeacanthus gaujicus* mazuļa skelets bez zvīņojuma seguma (arī mazākā līdz šim aprakstītā akantode paleontoloģiskajā hronikā). Tās ķermeni vietām klāj saglabājusies ķermeņa krāsviela, galvu iezīmē tikai acu krāsviela un nedaudzie branhiostegālie stari. Par akantodes esamību liecina labi attīstītie peldspuru dzelkšņi un lāpstiņu kauli. **A**, LDM 270/45 a; **B**, zīmējums pēc abām parauga pusītēm: LDM 270/45 a, LDM 270/45 b.

### 5.1.2. Systematic palaeontology

Class Acanthodii Owen, 1846
Order Acanthodiformes Berg, 1940
Family Mesacanthidae Moy-Thomas, 1939

## DIAGNOSES OF THE GENUS AND SPECIES

### Genus *Lodeacanthus* Upeniece, 1996

*Diagnosis.* Small, slender-bodied mesacanthid. Both jaws ossified as single units; upper jaw fenestrated, lower jaw without mandibular splint; mandibular joint simple. Enlarged dermal bones present in cheek and nasal regions; nasal bones crescent-shaped and paired. Hyoid operculum supported by numerous long branchiostegal rays, does not quite reach posterior end of gill region. No accessory gill covers.

Fin spines slender, straight or only slightly curved, ornamented on each side with a deep anterior groove followed by several fine, less pronounced grooves. Pectoral, dorsal and anal spines of about the same length, pelvic spines about one-third shorter. Dorsal spine situated slightly behind anal and shallowly inserted. One pair of intermediate fin spines, nearly half as long as pelvics. Caudal fin long, hypochordal lobe small and triangular; epicaudal lobe present, but very small. Scales unornamented.

### Species *Lodeacanthus gaujicus* Upeniece, 1996

*Diagnosis.* As for genus.

## DESCRIPTION

*Lodeacanthus gaujicus* is a small, fusiform mesacanthid; the largest completely preserved specimen is only 38.9 mm long; the estimated total body length of disarticulated one reaches 48.2 mm. The head plus gill region (prepectoral length) reaches approximately a quarter to third (22-33%) of the total specimen length. Fin-spine to body-length ratios are shown in Table 5.1. and schematic proportions in Figs. 5.3, 5.4. In adults of *Lodeacanthus* the head and the anal spine are comparatively larger than those in other members of the Mesacanthidae (Table 5.1 c and g). Related known mesacanthid genera represent also small sized acanthodians: in *Mesacanthus mitchelli* maximum length is 65.0 mm (Woodward, 1891), in *Triazeugacanthus affinis* 39.6 mm (Miles, 1966).

The schematic presentation of body proportions and indices (Figs. 5.3, 5.4) follows the scheme proposed by Zidek (1976, 1980). The prepectoral length was measured between the anterior margin of the head and the longitudinal axis of the scapula. The distances between the fin spines were measured between the anteriors of their proximal terminations. The fin spine lengths were measured between their proximal and distal terminations regardless of their slight curvature. The total specimen length was measured along the longitudinal body axis, summarizing the separate measurements between the elements. The number of scales per millimetre in a row (Y) is measured in the region of the largest/oldest trunk scales (caudally from the dorsal fin spine) in the natural (oblique) row, as it was proposed by Zidek (1976) and Zajic (1988).

Table 5.1. Proportions of *Lodeacanthus gaujicus* compared with those of members of Mesacanthidae and Acanthodidae (Upeniece, 1996, Table 1)
5.1. tabula. Akantodes *Lodeacanthus gaujicus* proporciju salīdzinājums ar Mesacanthidae un Acanthodidae pārstāvjiem (Upeniece, 1996, Table 1).

| *Measuring points* | Mesacanthidae | | | | | Acanthodidae | | |
|---|---|---|---|---|---|---|---|---|
| | **adult *Lodeacanthus gaujicus*** | | | *Triazeug-acanthus affinis*[1] | *Mesacanthus mitchelli*[2] | *Howittacanthus kentoni*[3] | *Acanthodes bridgei*[4] | *Acanthodes lundi*[5] |
| | number of measurem. | range | average | | | | | |
| a) $\frac{\text{pectoral-anal distance}}{\text{total specimen length}}$ | 3 | 0.37-0.40 | 0.38 | 0.31 | 0.32 | 0.38-0.47 | 0.42-0.51 | 0.46-0.52 |
| b) $\frac{\text{pelvic-anal distance}}{\text{total specimen length}}$ | 3 | 0.15-0.19 | 0.16 | 0.12 | 0.15 | 0.13-0.21 | 0.28-0.37 | 0.38-0.47 |
| c) $\frac{\text{prepectoral length}}{\text{total specimen length}}$ | 5 | 0.20-0.28 | 0.23 | 0.14 | 0.18 | 0.13-0.19 | 0.18-0.24 | 0.21-0.29 |
| d) $\frac{\text{pectoral spine length}}{\text{total specimen length}}$ | 4 | 0.12-0.18 | 0.15 | 0.11 | 0.15 | 0.14-0.17 | 0.17-0.20 | 0.15-0.20 |
| e) $\frac{\text{pelvic spine length}}{\text{total specimen length}}$ | 4 | 0.07-0.09 | 0.09 | 0.07 | 0.13 | 0.06-0.07 | 0.07-0.08 | 0.05-0.06 |
| f) $\frac{\text{dorsal spine length}}{\text{total specimen length}}$ | 4 | 0.14-0.17 | 0.15 | 0.12 | 0.14 | 0.10-0.12 | 0.12-0.14 | 0.12-0.13 |
| g) $\frac{\text{anal spine length}}{\text{total specimen length}}$ | 3 | 0.13-0.15 | 0.14 | 0.10 | 0.12 | 0.12-0.14 | 0.12-0.14 | 0.11-0.16 |
| h) $\frac{\text{pelvic spine length}}{\text{pectoral spine length}}$ | 4 | 0.54-0.63 | 0.60 | 0.68 | 0.89 | 0.41-0.46 | 0.17-0.20 | 0.27-0.35 |
| i) $\frac{\text{dorsal spine length}}{\text{pectoral spine length}}$ | 3 | 0.88-1.02 | 0.97 | 1.11 | 0.94 | 0.57-0.75 | 0.64-0.74 | 0.62-0.63 |
| j) $\frac{\text{anal spine length}}{\text{pectoral spine length}}$ | 2 | 1.02-1.17 | 1.10 | 0.97 | 0.83 | 0.71-0.88 | 0.64-0.74 | 0.72-0.77 |

**1** - measuruments from reconstructions in Miles, 1966; **2** - measuruments from reconstructions in Watson, 1937; **3** - data and measuring points from Long, 1986; **4, 5** - data and measuring points from Zidek, 1985.

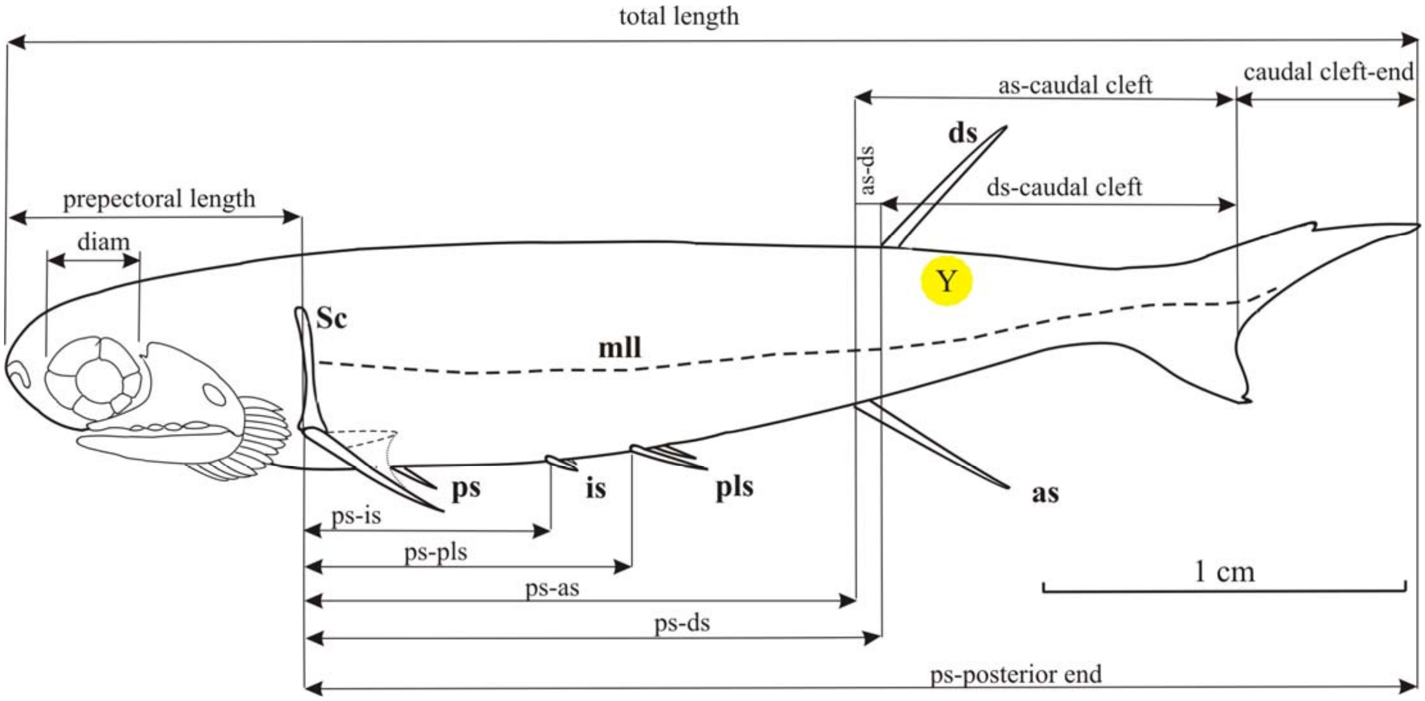


Fig. 5.3. Reconstruction of mesacanthid *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 4, with slight modifications) and indicated distances: **as-caudal cleft**, distance from anal spine to caudal cleft; **as-ds**, distance between anal and dorsal spines; **diam**, outer diameter of circumorbital ring; **ds-caudal cleft**, distance from dorsal spine to caudal cleft; **ps-as**, distance between pectoral and anal spines; **ps-ds**, distance between pectoral and dorsal spines; **ps- posterior end**, distance from pectoral spine to tip of tail; **ps-is**, distance between pectoral and intermediate spines; **ps-pls**, distance between pectoral and pelvic spines. **Y -** number of scales per millimetre in a natural, oblique row (postdorsal-precaudal region).

5.3. att. Mezakantīda *Lodeacanthus gaujicus* rekonstrukcija (Upeniece, 1996, Fig. 4, ar nelielām izmaiņām) un mērītie attālumi: **as-caudal cleft**, attālums no anālās peldspuras dzelkšņa līdz *caudal cleft*; **as-ds**, attālums starp anālo un dorsālo peldspuru dzelkšņiem; **diam**, cirkumorbitālā gredzena ārējais diametrs; **ds-caudal cleft**, attālums no dorsālās peldspuras dzelkšņa līdz *caudal cleft*; **ps-as**, attālums starp krūšu un anālo peldspuru dzelkšņiem; **ps-ds**, attālums starp krūšu un dorsālo peldspuru dzelkšņiem; **ps-posterior end**, attālums no krūšu peldspuras dzelkšņa līdz astes galiņam; **ps-is**, attālums starp krūšu un starpspuru peldspuru dzelkšņiem; **ps-pls**, attālums starp krūšu un iegurņa peldspuru dzelkšņiem; **Y** – zvīņu skaits vienā milimetrā (dorsāli-prekaudālā reģionā).

### Head and visceral skeleton

The dorsal surface of the head is covered by enlarged scales and irregularly shaped tesserae. The tesserae covering extends from between the orbits into the nasal region and is best seen in specimens LDM 270/5 and LDM 270/40 (Fig. 5.5 A,B). The longitudinal length of tesserae is ranging from 0.1 to 0.3 mm.

Fragments of the **neurocranium** are well marked by their red-brownish colour in ten specimens (Table 5.2): in larger juveniles and in adults, but they are too poorly preserved to reveal any salient features (Figs. 5.1 B, 5.2, 5.6 A, 5.7, 5.22). Two youngest juveniles (LDM 270/45, 47) without squamation extent reveal light coloured mass – possible remains of neurocranium - located directly behind the eye staines. Some specimens reveal it bilateral located directly behind the eys (270/39) or the eys staines (270/45).

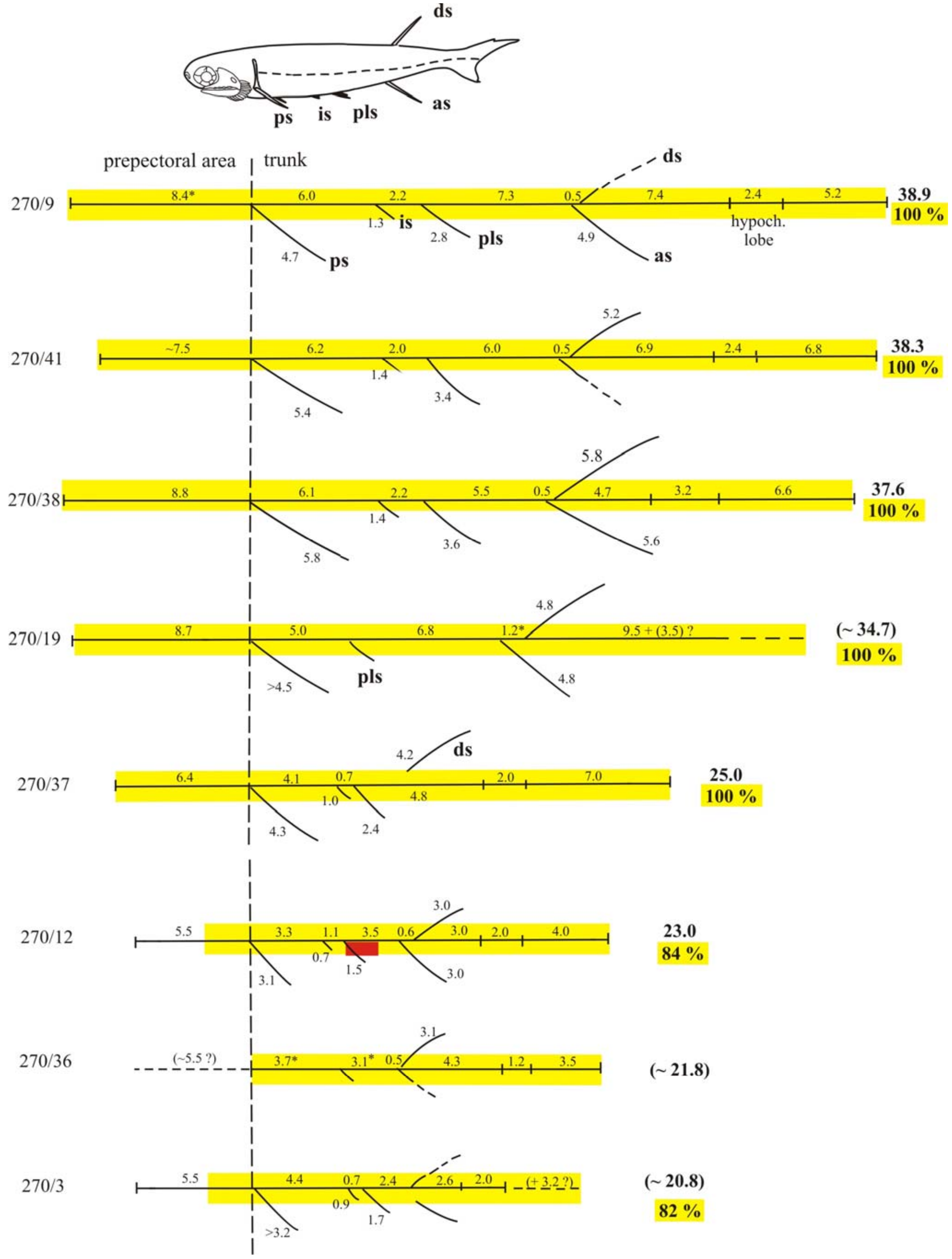
**The cheek region** is covered by enlarged, but very thin, imbricating scales. **Dermal cheek bones** are preserved in 8 specimens (Table 5.2). These bones are located in a row, and they are so thin that their exact shape and number cannot be determined. One elongated dermal cheek bone is situated near the mandibular joint and a row of at least 7 much smaller dermal bones is located anteriorly (Fig. 5.6). The row of them is best seen in juvenile specimens in which the scale covering of the head had not been yet developed. In adults only the largest dermal cheek bone (the above mentioned elongated one) is recognised on each side near the mandibular joint (LDM 270/5).

**Branchiostegal rays** are more-or-less straight and closely spaced (Figs. 5.3, 5.6), and bear a very fine longitudinal ridge on the outer surface. They are longer and more numerous than in *Triazeugacanthus,* but shorter than in *Mesacanthus*. The position of branchiostegal rays is similar to *Mesacanthus mitchelli,* but differs in that they extend below the lower jaw only along one-quarter of its length (best seen in specimens LDM 270/2, 5, 9, 18, 19, 23, 34, 37, 40). Altogether they are visible in 14 specimens (Table 5.2).

Table 5.2 Summary on preserved skeletal elements of *Lodeacanthus gaujicus*
5.2. tabula. Pārskats par akantodēs *Lodeacanthus gaujicus* konstatētajiem skeleta elementiem

| Skeletal elements | **Number of specimens** LDM 270/... |
|---|---|
| 1. Circumorbital bones | **2**, 3, 4, 5, 7, **17**, **19**, **22**, 28, **31**, 33, 34, 35, 37, 40, 43, 60 |
| 2. Nasal bones | 2, 4, 5, 7, 12, 19, **22**, **28**, **33**, **34b**, 37, **40**, **41**, **46** |
| 3. Cheek bones | 2, 3, **5**, **12**, 31, 37, 38, **46** |
| 4. Branchiostegal rays | **2**, **5**, 7, 9, 18, **19**, **23**, **34**, 35, 37, **39**, **40**, 49, 60 |
| 5. Tesserae | 2, 3, **5**, 12, 19, **35**, 37, 38, **40** |
| 6. Scapula | **2**, 3, 5, 12, **14**, **18**, 21, 23, 26, 28, 35, 36, 37, 38, 39, 40, 42, 43, 45, 46 |
| 7. Palatoquadratum | 2, 17, 19, **29**, **30**, **34a**, 40, 42, 43a |
| 8. Meckelian element | 2, **5**, 8, 9, 14, 18, 19, 26, 34, **38**, 40, 42 |
| 9. Branchial arches | 2, 8, **14**, 34, 39 ?, 40 ? |
| 10. Endocranium (patches) | 2, 3, 9, 14, 22, 28, 35, 37, 38, 39 |
| 11. Vertebral column (?) | **38** |
| 12. Main lateral line | **12**, 13, 22, 25, 38, 44 |
| 13. Infraorbital sensory line | 3, **12**, 23, 37, **46** |
| 14. Unidentified elements on the posterior end of the palatoquadratum | **14**, 40 |
| 15. Pectoral fin | 14, **26**, 39 |
| 16. Film of skin on the body | **1**, 12, **22**, 23, 25, **28**, **44**, **45** |

(in bold – the best preserved ones)


ds
ps
is
pls
as
prepectoral area
trunk
ds
270/9
8.4*
6.0
2.2
7.3
0.5
7.4
2.4
5.2
38.9
100 %
1.3
is
2.8
pls
4.9
as
hypoch.
lobe
4.7
ps
270/41
5.2
~7.5
6.2
2.0
6.0
0.5
6.9
2.4
6.8
38.3
100 %
1.4
3.4
5.4
270/38
5.8
8.8
6.1
2.2
5.5
0.5
4.7
3.2
6.6
37.6
100 %
1.4
3.6
5.6
5.8
270/19
4.8
8.7
5.0
6.8
1.2*
9.5 + (3.5) ?
(~ 34.7)
100 %
pls
>4.5
4.8
270/37
4.2
ds
6.4
4.1
0.7
2.0
7.0
25.0
100 %
1.0
4.8
4.3
2.4
270/12
3.0
5.5
3.3
1.1
3.5
0.6
3.0
2.0
4.0
23.0
84 %
0.7
1.5
3.1
3.0
270/36
3.1
(~5.5 ?)
3.7*
3.1*
0.5
4.3
1.2
3.5
(~ 21.8)
270/3
5.5
4.4
0.7
2.4
2.6
2.0
(+ 3.2 ?)
(~ 20.8)
82 %
0.9
1.7
>3.2

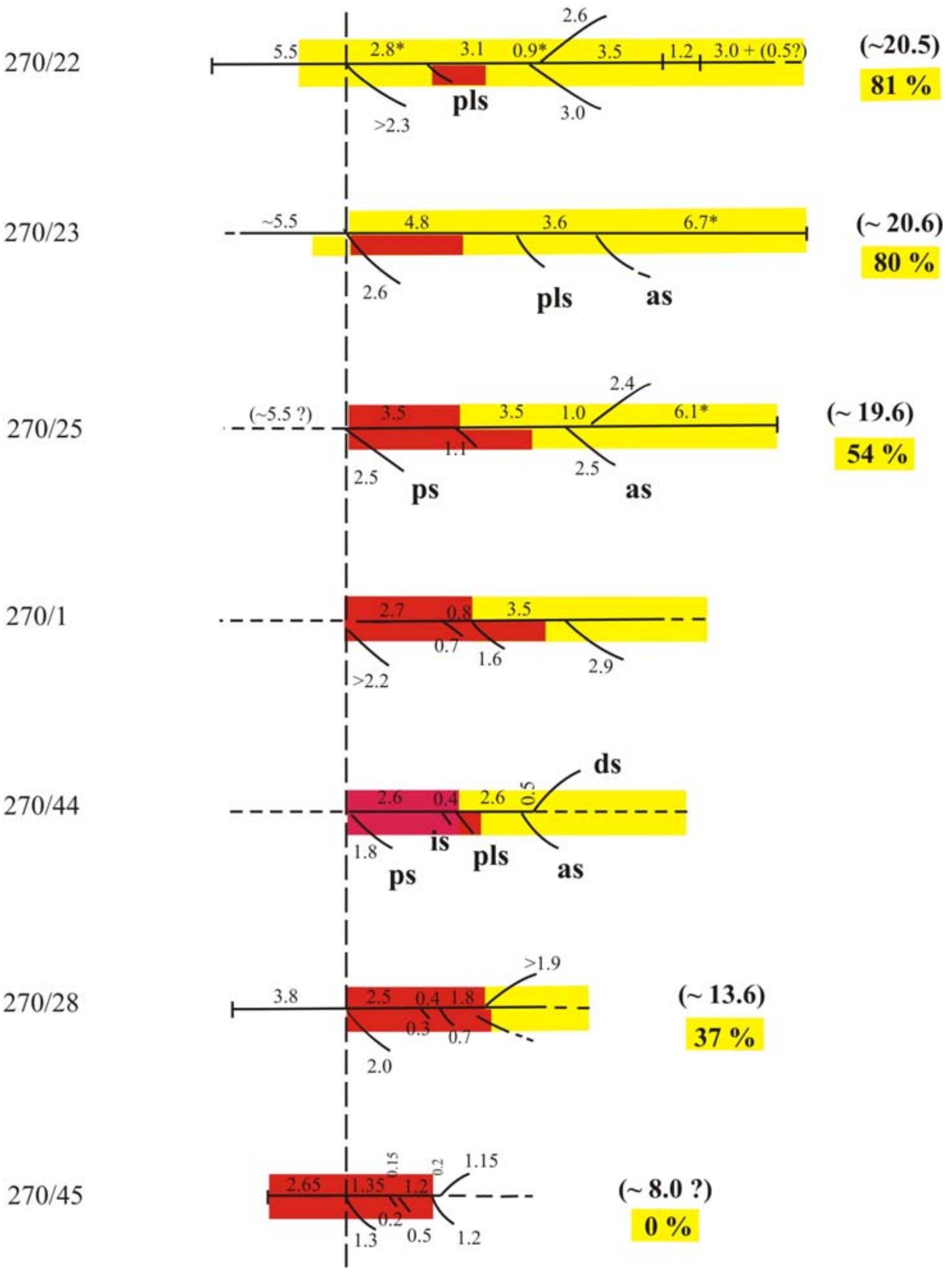


Fig. 5.4. Schematic presentation of proportions of the body and squamation extent (in yellow) of the most complete specimens in *Lodeacanthus gaujicus* (Upeniece, 1996, Fig.3, with modifications). Red strips indicate well marked unsquamated region, covered by film of skin (above the black horizontal line - in the dorsal part, below - in the ventral part of the body). Vertical interrupted line divides all bodies into a prepectoral region (the head + gill chamber, to the left) and a trunk (to the right). Specimen numbers to the left. Values in parentheses mean the estimated total specimen length unlike the measured values. Approximate measurements denoted by asterik. Measurements in mm.

5.4. att. Vislabāk saglabājušos akantožu *Lodeacanthus gaujicus* ķermeņa proporciju un zvīņojuma attīstības (dzeltenās joslas) shematisks attēlojums (Upeniece, 1996, Fig.3, ar izmaiņām). Sarkanās joslas norāda uz ķermeņa daļām, kuras ir segtas tikai ar ķermeņa membrānu, un uz tām vēl nav attīstījies zvīņojums (virs melnās horizontālās līnijas – muguras pusē; zem – vēdera pusē). Vertikālā pārtrauktā līnija sadala visus skeletus pirmspektorālajā reģionā (galva + žaunas) un rumpī. Paraugu numuri kreisajā pusē. Skaitļi iekavās nozīmē teorētiskos ķermeņu garumus. Aptuveni mērījumi atzīmēti ar zvaigznītēm. Mērījumi milimetros.

A pair of enlarged **nasal bones** (Fig. 5.5) partially surrounds the nares. These bones are preserved in 14 specimens (Table 5.2) including some of the smallest juveniles (Fig. 5.20), but their paired arrangement and orientation are visible only in LDM 270/22, 28, 34, 46 (Figs. 5.5 C, 5.6, 5.20). They are crescentic to semi-circular with the undulate convex margin facing upward and a relatively pronounced ridge situated mesially (LDM 270/2, 5, 7). The bone have thickening on the outer surface around the nasal openings (LDM 270/28, 40). The presence of a pair of nasal bones differs *Lodeacanthus* from the related genus *Triazeugacanthus* and *Mesacanthus*.

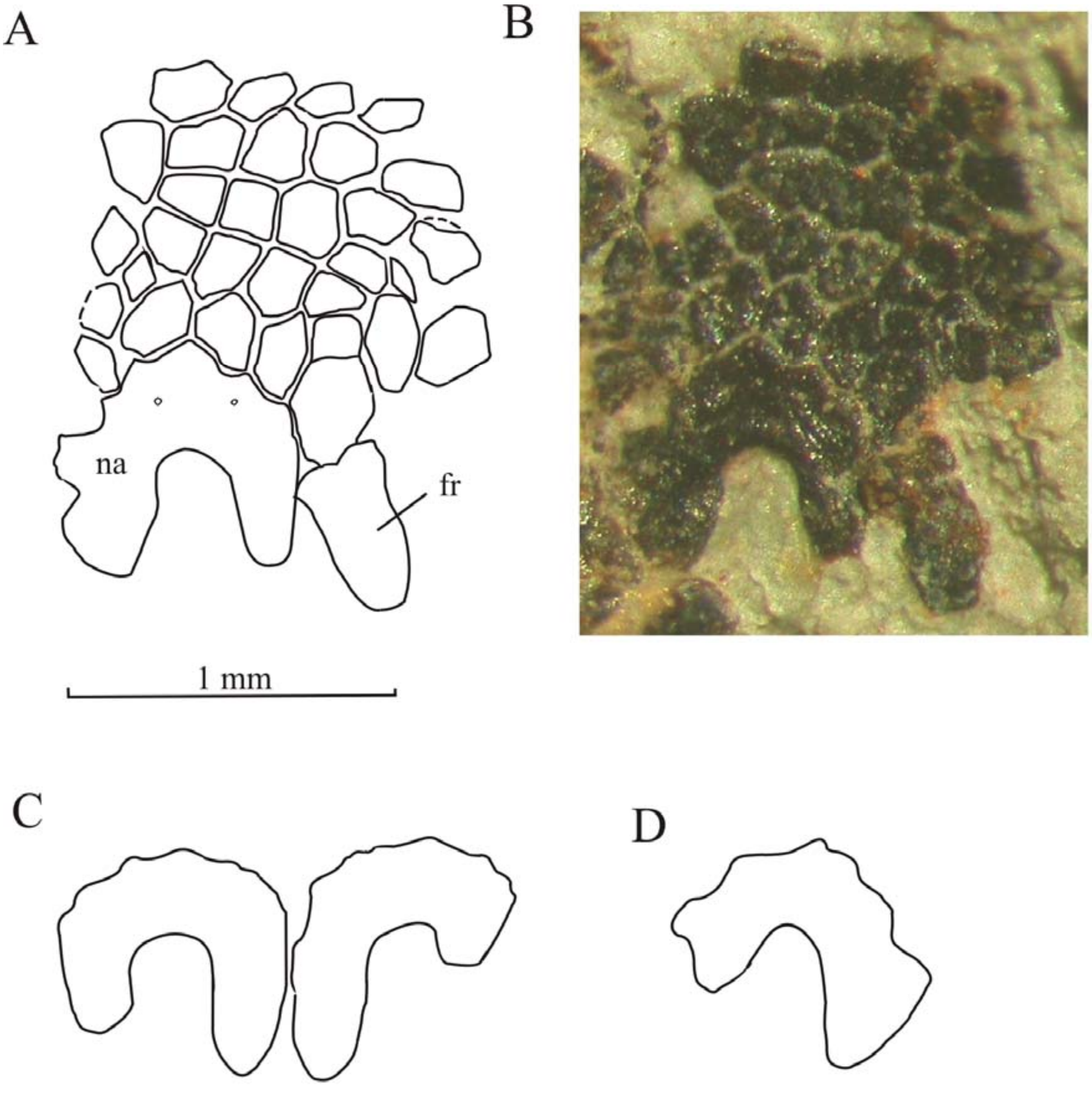


Fig. 5.5. Nasal bones of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1 E, F, G). **A, B,** with surrounding tesserae, specimen 270/40a; **C,** a pair of bones, 270/34b, **D,** detached bone, 270/7a.

5.5. att. Akantodes *Lodeacanthus gaujicus* nazālie kauli (Upeniece, 1996, Fig. 1 E, F, G). **A, B**, ar aptverošām tesērām, paraugs LDM 270/40a; **C**, nazālo kaulu pāris, LDM 270/34b; **D**, atsevišķs nazālais kauls, LDM 270/7a.

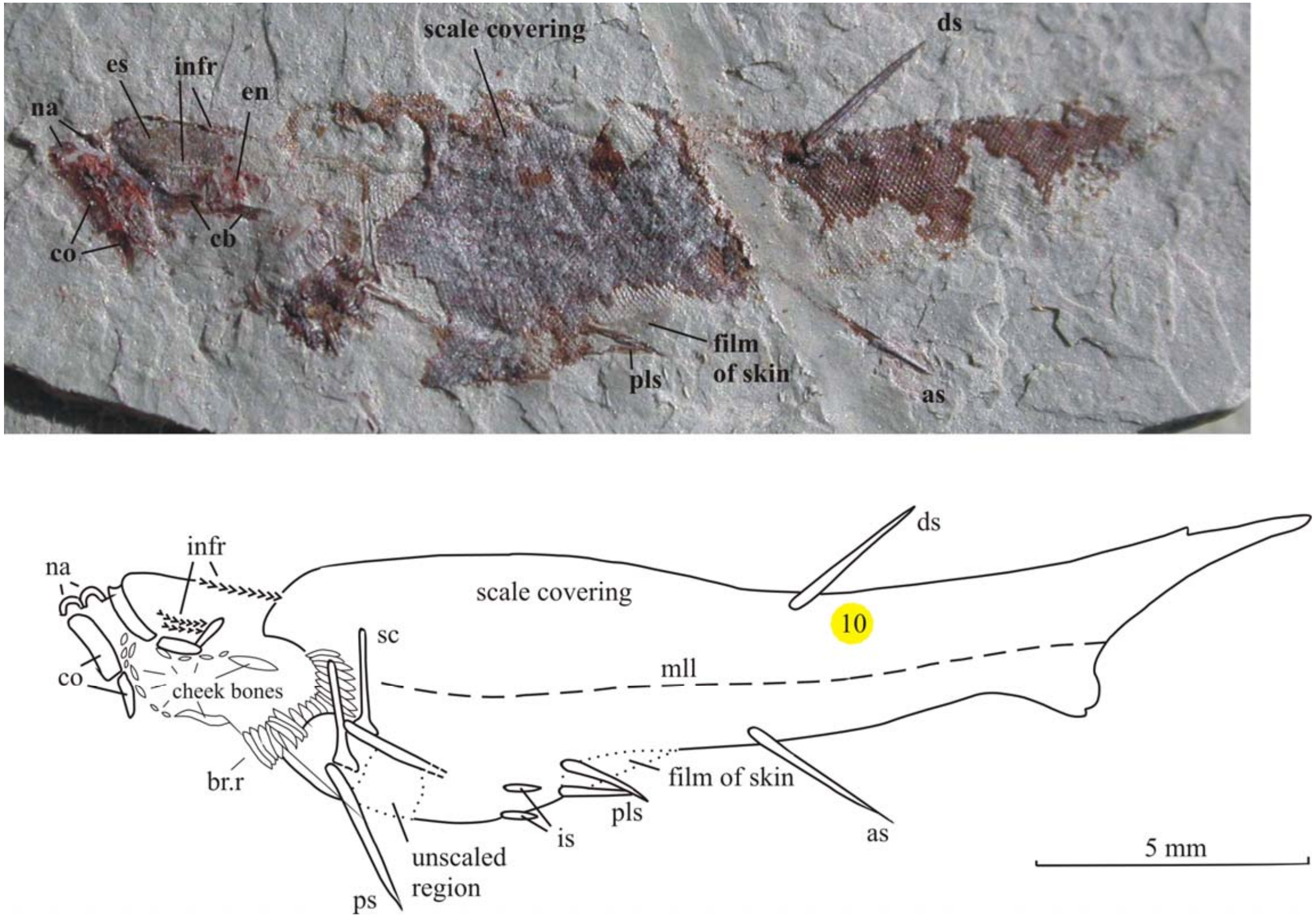


Fig. 5.6. Juvenile individual of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 2 A, Pl. 1, Fig. 3) LDM 270/12 (total length 23.0 mm). Squamation reaches endocranium (en), squamation extent 84% (see also Fig. 5.4). Drawing compiled from part (LDM 270/12a) and counterpart (LDM 270/12b).

5.6. att. Akantodes *Lodeacanthus gaujicus* mazulis (Upeniece, 1996, Fig. 2 A, Pl. 1, Fig. 3) LDM 270/12 (kopgarums 23.0 mm). Zvīņojums sasniedzis endokrānija reģionu (en), zvīņojuma segums 84% (skatīt arī 5.4. att.). Zīmējums pēc abām parauga pusēm (LDM 270/12a; LDM 270/12b).

The **circumorbital bones** are preserved in 18 specimens (Table 5.2). The circumorbital ring (Fig. 5.7) is composed of presumably six, transversely arched dermal bones (in *Triazeugacanthus* there are 4 or 5 bones, in *Mesacanthus* – 5 bones) that bear a very fine concentric ornament of ridges. According to Miles (1966) the circumorbital plates of *Triazeugacanthus affinis* have an ornament of shallow pits. In *Lodeacanthus* the ridges issue from a centre situated closer to the inner margin of each bone. The anterodorsal and anteroventral bones are the largest, whereas the posterior ones are the smallest. The number of circumorbital bones increases during the ontogeny: from four (Fig. 5.20) to five (LDM 270/22) and presumably to six (Fig. 5.7. A).

The outer diameter of the ring can be measured in adults (LDM 270/2, 270/19) and in juveniles (LDM 270/3, 270/22) in which it forms, respectively, 29% and 33% of the prepectoral length. The dark-coloured eye stain is usually preserved at the circumorbital ring of juveniles (Figs. 5.2, 5.6 A, 5.20). In adults the head is covered by the squamation and eye stains can not be visible.

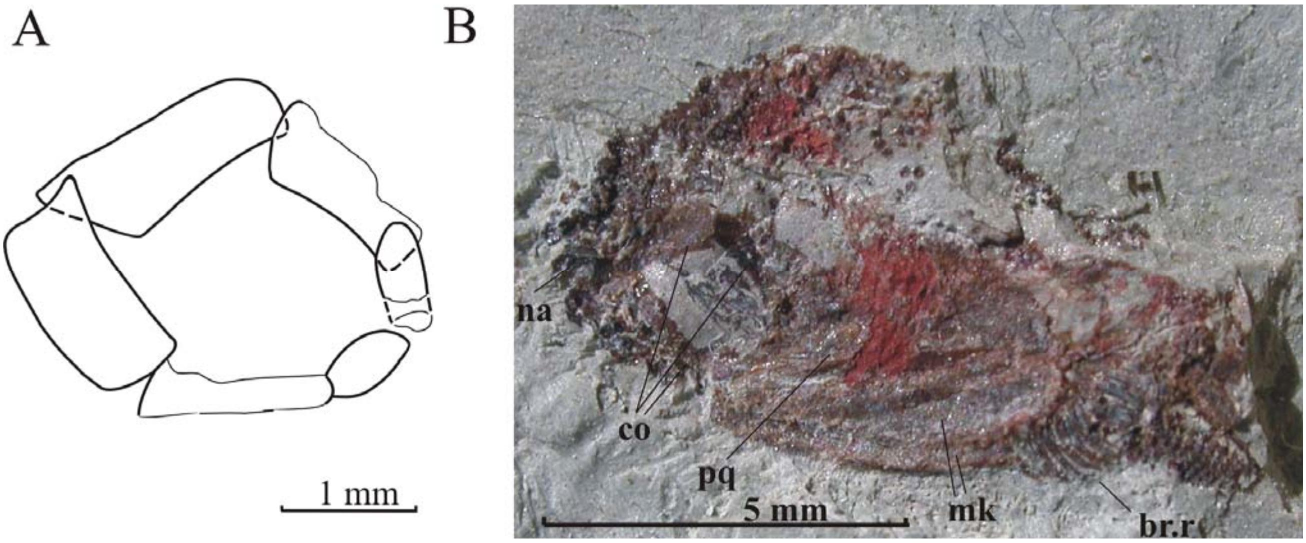


Fig. 5.7. **A,** Circumorbital ring of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1 H); inside view, after part and counter part: LDM 270/2 a, 270/ b. Thick lines = natural borders, thin lines = preserved borders. Presumably six circumorbital bones are preserved. **B,** head of the same specimen, LDM 270/2 b. Redish patches presumably are fragments of the neurocranium.

5.7. att. **A**, Akantodes *Lodeacanthus gaujicus* cirkumorbitālie (acu) kauli (Upeniece, 1996, Fig. 1H) in visceral view, pēc abām parauga pusītēm (LDM 270/2a; LDM 270/2b). Biezās līnijas = kaulu dabīgās robežas, plānās līnijas – kaulu redzamās robežas. Domājams, ka ir saglabājušies seši acu kauli. **B**, galva no tā paša parauga, LDM 270/2b. Sarkanīgie plankumi, iespējams, ir smadzeņu kapsulas atlieku fragmenti.

**The palatoquadrate** (Fig. 5.8. A,B) is ossified (co-ossified) as a single unit and has a vacuity similar to that in *Cheiracanthus latus*, but located more posteriorly (Watson, 1937, Fig. 13). One detached palatoquadrate (Fig. 5.8 A) bears a second vacuity whose margins may or may not be natural, and it is possible that the opening results from post-morten abrasion. The anterior end is elongated and bears a weakly developed basal process, the suborbital part is short and slender, and the postorbital part is deep, with a prominent extrapalatoquadrate ridge which ends in the articulation area. The collection includes two detached upper jaws (LDM 270/29, 30), as well as 7 articulated ones (LDM 270/2, 17, 19, 34, 40, 42, 43).

**The lower jaw** (Fig. 5.8 C) is preserved in 12 specimens (Table 5.2), in all of which the Meckelian element is ossified (co-ossified) as a single unit and shows no evidence of a mandibular splint or attachment area for that dermal element. It can thus be stated quite unequivocally that *Lodeacanthus* did not possess a mandibular splint. The upper margin of the Meckelian element is nearly flat, whereas the lower margin is distinctly convex. There is no preglenoid process. The joint consists of a lateral articular cotylus and a medial prearticular cotylus, which interlock, with the articular and prearticular processes of the palatoquadrate forming the mandibular joint of simple type.

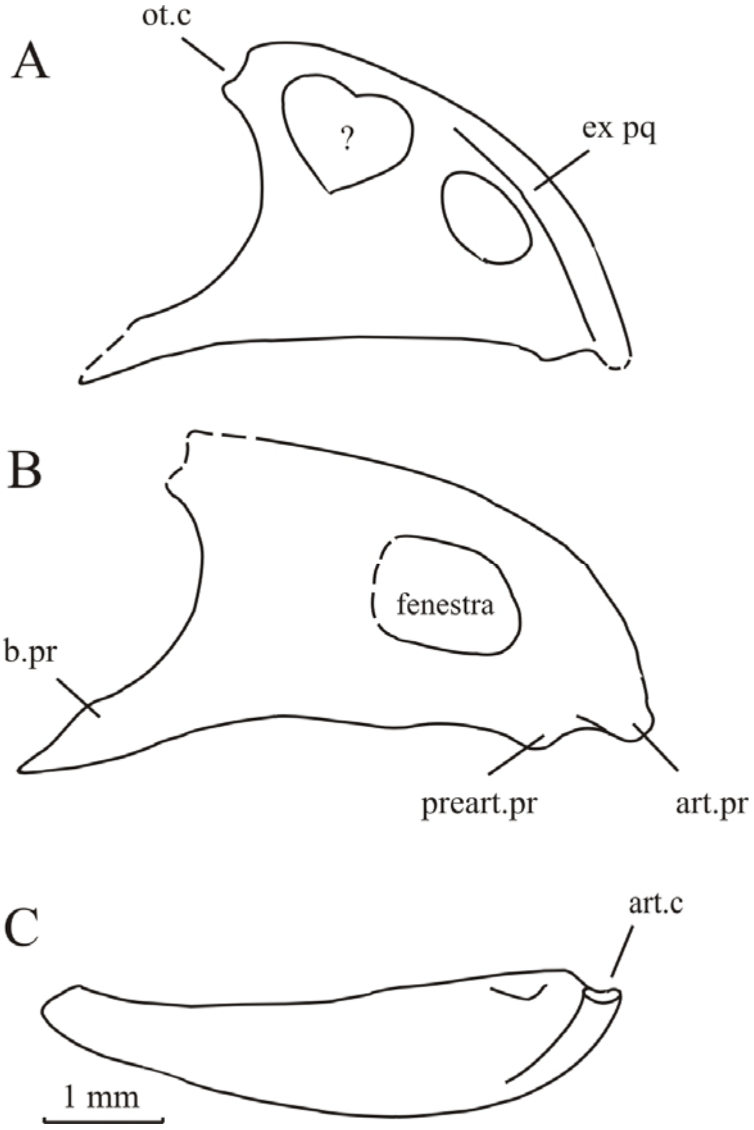


Fig. 5.8. Jaws of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig.1 B-D). **A, B,** upper jaws (palatoquadrates) of specimens LDM 270/29 and 270/30; **C,** lower jaw (Meckelian cartilage), LDM 270/40.

5.8. att. Akantodes *Lodeacanthus gaujicus* žokļu kauli (Upeniece, 1996, Fig.1 B-D). **A,B**, augšžokļi (aukslēju-kvadrāta kauli), paraugi LDM 270/29 un LDM 270/30; **C**, apakšžoklis (Mekeļa skrimslis), LDM 270/40.

**The scapula** has a long, slender dorsal division and an expanded ventral region of approximately triangular shape (Figs. 5.6, 5.9). The ventral trianguloid region accounts for about one-fifth of the height of the scapula (Upeniece, 1996). In *Triazeugacanthus,* according to Miles (1966), it accounts for about one-quarter, but in *Mesacanthus* (after Watson's reconstruction, 1937), two-thirds. In adults the ventral region is more prominent (specimens LDM 270/14, 18, 38, 39, 42) than in juveniles. It is concave from visceral surface, with processes on the anterior and posterior edges, and convex from outer surface (in Fig. 5.9 it is flattened). The scapular blade is nearly circular in cross-section. In juveniles and subadults (specimens LDM 270/3, 12, 21, 28, 36, 45, 46) the scapula is flat (it could be due to fossilization process). Altogether the scapula is visible in 20 specimens (Table 5.2). In the smalest specimen (LDM 270/45) the scapula is rather stout and represents a equilateral triangle (Fig. 5.2).

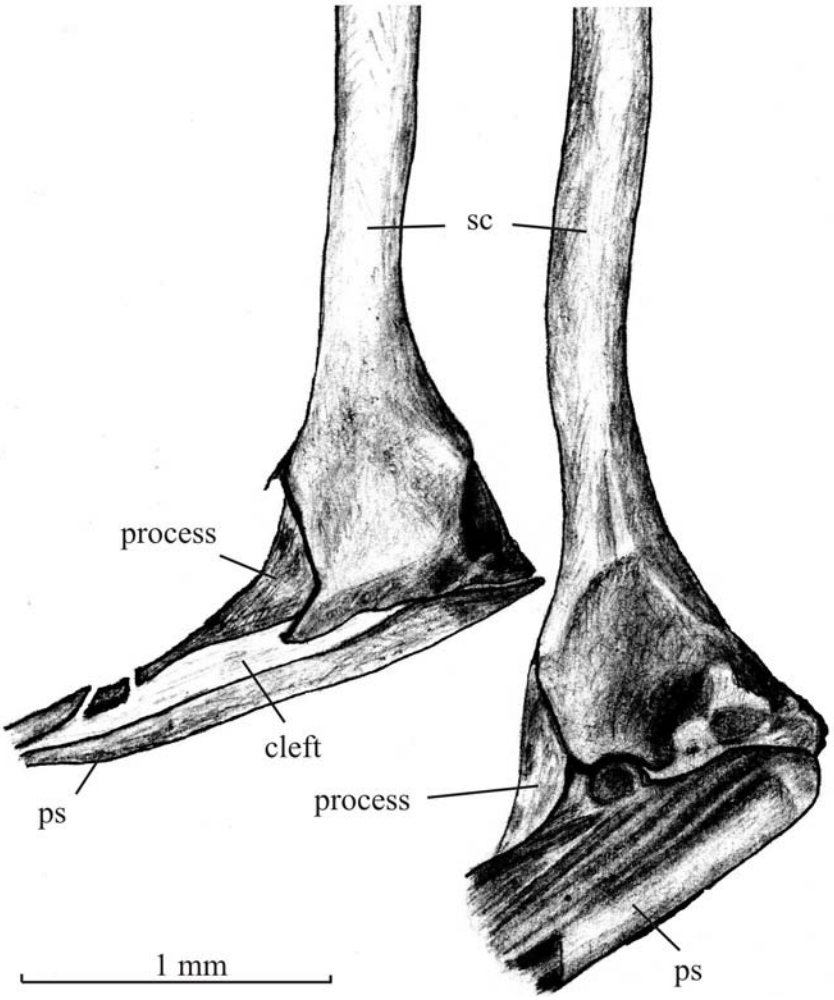


Fig. 5.9. Articulation area of scapula and pectoral fin spine in *Lodeacantus gaujicus* (Upeniece, 1996, Fig. 1 J). Specimen LDM 270/18 a.

5.9. att. Lāpstiņas kaula un krūšu peldspuras dzelkšņa artikulācijas reģions akantodei *Lodeacantus gaujicus* (Upeniece, 1996, Fig. 1 J). Paraugs LDM 270/18 a.

The height of the scapula attains 40-88% of the pectoral spine length in all studied specimens, both juveniles and adults (LDM 270/2, 3, 5, 12, 14, 23, 26, 28, 37, 38, 42, 45). The relative length of the scapula increases during the ontogeny. It was the first component of the endoskeleton to ossify, followed by jaws and then the branchial arches.

Only one specimen (LDM 270/18) was available for detailed study of the articulation area (Fig. 5.9). There is a small process situated on the pectoral spine's dorsal surface; the ventral region of the scapula has a ventral mesial opening. The process sat within this opening.

**Branchial arches** are visible in four specimens (Table 5.2). The identification of their segments cannot be established, but it nevertheless appears that five pairs are present (Fig. 5.10). The anterior part of the tallest of them bears a clearly visible deep notch; the posterior ones are stout and projected posteriorly. Several horizontally located elements of the arch are recognized. Two specimens (LDM 270/14 and LDM 270/40) show some unidentified small bones located on the posterior margin of the palatoquadrate (Fig. 5.10): possible attachments for the branchiostegal rays (?).

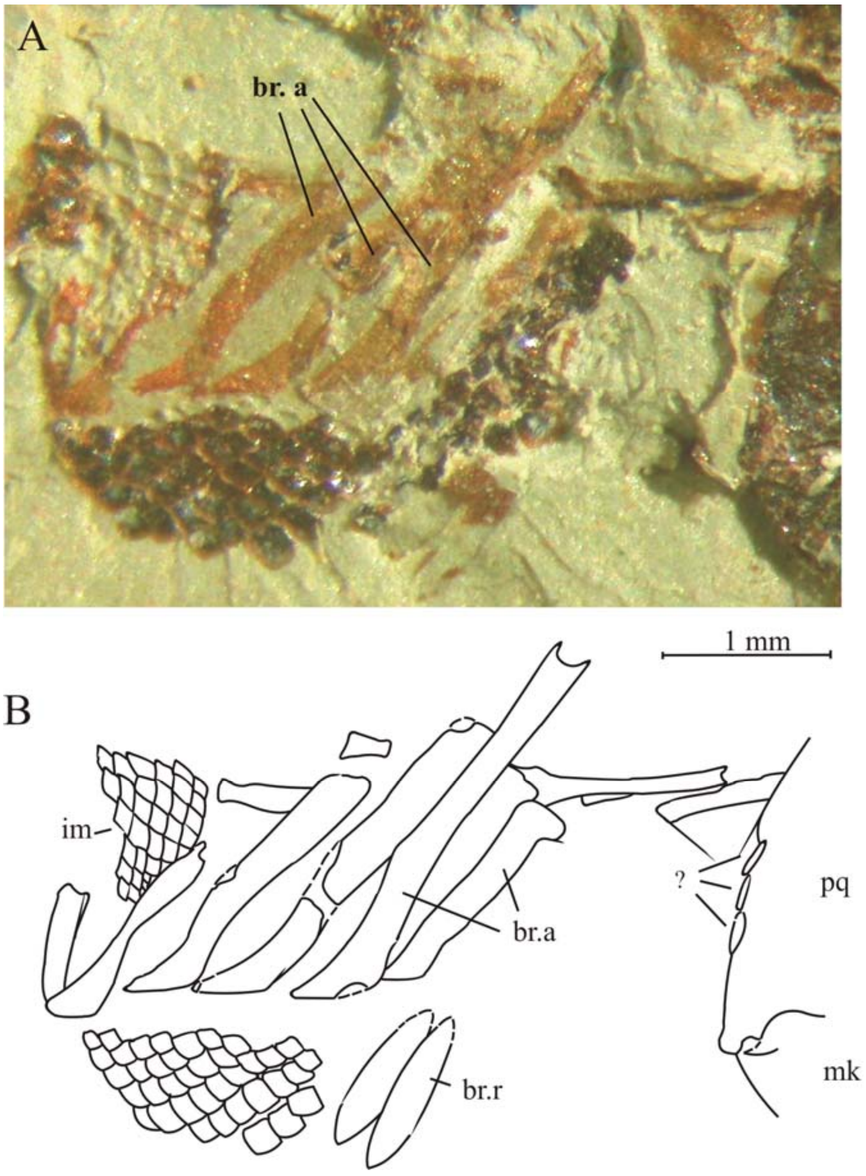


Fig. 5.10. Fragment of posthyoidean branchial arches of left side of *Lodeacanthus gaujicus*, lateral view. At least five pairs are present. Question mark points to unknown small bones. Specimen LDM 270/14. **A**, photo; **B**, drawing (Upeniece, 1996, Fig. 1 I).

5.10. att. Piecu žaunu loku fragmenti akantodei *Lodeacanthus gaujicus*, sānskats, kreisā puse. Jautājuma zīme norāda uz nezināmiem elementiem. Paraugs LDM 270/14. **A**, fotogrāfija; **B**, zīmējums pēc tā paša parauga (Upeniece, 1996, Fig. 1 I).

### Fins and fin spines

**Fins.** In adults the covering of the very fine scales on the **pectoral fins** (zone 5 in Fig. 5.15) is preserved (specimens LDM 270/14, 26, 39). The pectoral fin is narrow-based. There is a longitudinal opening (cleft) for the fin located on the pectoral spine's posterior margin (Fig. 5.9). The opening reaches 29-34% of spine length in four specimens measured (LDM 270/2, 14, 26, 42, 43). There is a row of small openings distally to the mentioned cleft (LDM 270/18, 26a, 41). This row must have served for the attachment of the unpreserved fin lobe. Such fin clefts and a row of small openings are visible also on the pelvic and anal spines (both in specimen LDM 270/26b).

The **caudal fin** is preserved in ten specimens (LDM 270/9, 10, 11, 12, 13, 22, 27, 36, 37, 38) in which the distance from the cleft to the tip of the axial lobe is 2.6-8.6 mm (Figs. 5.4, 5.11). The ratio of axial-lobe length to total length of specimen varies between 0.13 and 0.20 in five measured specimens (LDM 270/9, 12, 22, 37, 38). In adult individuals (LDM 270/9, 38) the hypochordal lobe is triangular (Figs. 5.1 B, 5.22), but in juveniles the margins are rather rounded (Fig. 5.6). Such rounded margins are visible also in the two detached caudal fins (Fig. 5.12); the number of scales per mm (8 and 10 respectively) indicate their belonging to the subadult-adult transition stage (Table 5.3), but distance measurements of the caudal part (Fig. 5.11) – to the subadult stage. Above mentioned features indicate that these disarticulated specimens in Fig. 5.4 could have been placed between articulated ones of LDM 270/37 and 270/12).

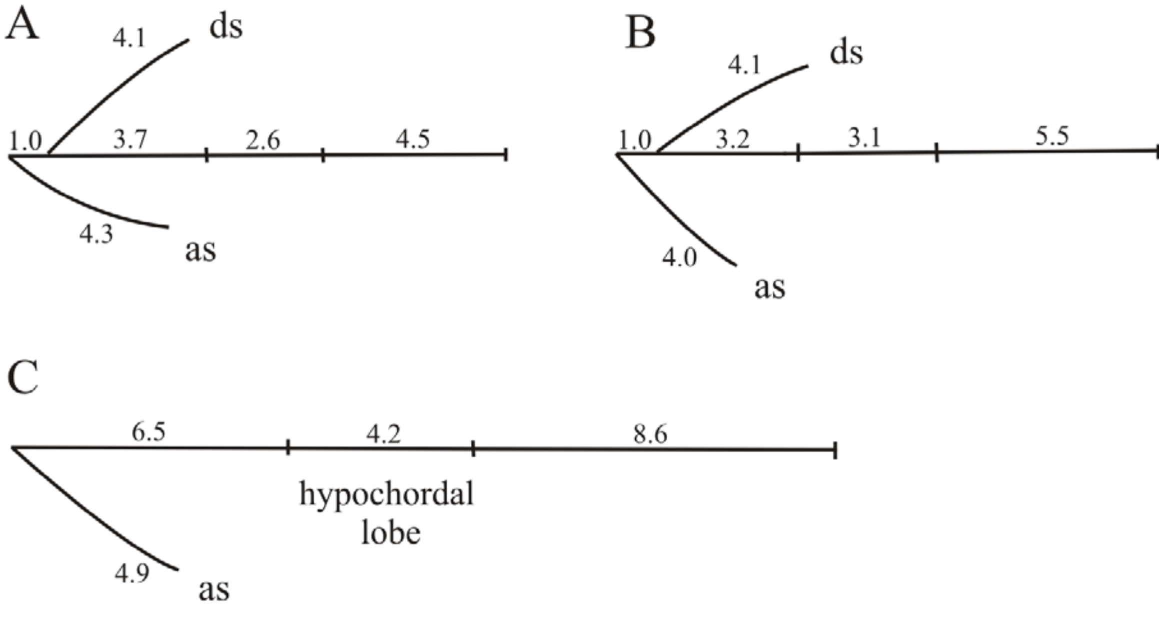


Fig. 5.11. Schematic presentation of proportions of caudal part of squamated, incompletely preserved individuals of *Lodeacanthus gaujicus* (Upeniece, 1996, part of Fig. 3). A, LDM 270/11. B, LDM 270/13. C, LDM 270/10.

5.11. att. Nepilnīgi saglabājušos akantožu *Lodeacanthus gaujicus* kaudālās daļas proporciju shematisks attēlojums (Upeniece, 1996, daļa no Fig. 3). A, LDM 270/11. B, LDM 270/13. C, LDM 270/10.

The caudal fin differs considerably from that in *Triazeugacanthus*. It has a small notch on the ventral end of the hypochordal lobe, and an epichordally situated row of thin, slightly enlarged, but thinner scales, best seen in holotype LDM 270/38 and in LDM 270/9a. These scales took part in a forming of a very small epichordal lobe, as it is known in *Mesacanthus mitchelli* (Watson, 1936, Fig. 8).

The epichordal lobe could coinside with a zone-2 (following the terminology of Heyler, 1969, Fig. A), described by Zidek (1976) for *Acanthodes:* the presence only of this zone (without yet undeveloped Z-2`` zone) suggests some immaturity (Zidek, 1976, Fig. 11 C). Therefore the largest articulated specimen (38.9 mm) could be nearly mature individual. Estimated total length of the largest known, but disarticulated individual (Fig. 5.11, specimen LDM 270/10) could have been 48.25 mm as the ratio of dorsal spine distance to total body length remains constant reaching about 40% (Table 5.5, in green).

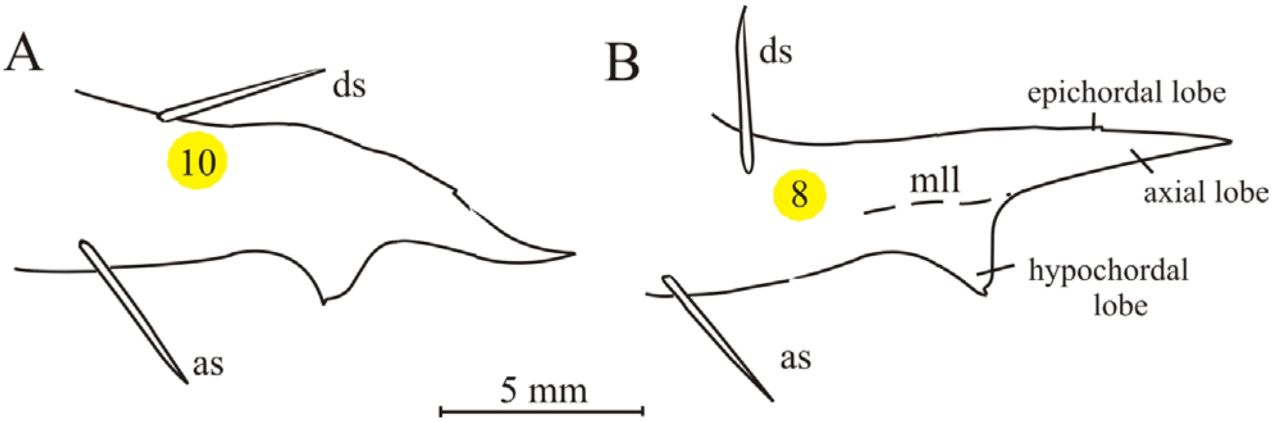


Fig. 5.12. Caudal fins of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 2 C, D with slight modifications). **A,** Presumably subadult-adult transition stage individual, LDM 270/11; **B,** presumably adult individual, LDM 270/13.

5.12. att. Akantodes *Lodeacanthus gaujicus* kaudālās peldspuras (Upeniece, 1996, Fig. 2 C, D, ar izmaiņām). **A**, domājams, pusaudža - pieauguša īpatņa starpstadija, LDM 270/11; **B**, domājams, pieaudzis īpatnis, LDM 270/13.

The **fin spines** (Figs. 5.1, 5.2, 5.3, 5.6, 5.12, 5.21) are slender, straight or slightly curved, and ellipse-shaped in cross-section; they are ornamented on each side with a deep anterior groove followed by several fine, less pronounced grooves, and the distal end is ornamentated.

The fin spines lack the specially developed insertion areas and no particularly arranged scales around the insertion area can be marked. The dorsal and anal spines were most suitable for measurements of the spine`s insertion length: the ratio of the insertion length to the total spine length comprises 0.16 in four specimens measured (LDM 270/9, 11, 12, 36) and reaches 0.23 in specimen LDM 270/38 (Fig. 5.22).

**Pectoral, dorsal and anal spines** are of about the same length, pelvic spines are about one-third shorter. Dorsal spine is situated slightly behind the anal spine (Figs. 5.2, 5.3, 5.4, 5.6, 5.22). One specimen shows well marked red patch (Fig. 5.22 A) above the insertion area of the anal spine – possible remains of support element of the fin spine.

The **pelvic fin spines** are situated nearly halfway between the pectorals and anal fin spine (Fig. 5.1 B), in some specimens closer to the anal or pectoral fin spine (Fig. 5.4). In adults (specimens LDM 270/9, 37, 38, 41) they are 54-63% as long as the pectorals (Table 5.1), 35-51% as long in juveniles (LDM 270/12, 25, 28, 45).

The **intermediate fin spines** are short (but approximately twice as long as in *Triazeugacanthus,* Gagnier, pers.comm. in Upeniece, 1996), flat and rather broad, and ornamented only by some fine grooves. Their length is nearly half that of the pelvic spines. They are placed closer to the pelvic than the pectoral fins (73-86% of the distance from the pectoral to the pelvic spines).

In adult individuals the length of pectoral, dorsal and anal fin spines is up to 5.8 mm, of pelvic fin up to 3.6 mm and of the intermediate fin up to 2.4 mm (Upeniece, 1996).

In juveniles the pectoral (ps, Fig. 5.20), pelvic and intermediate fin spines have a row of small denticles on the end of the anterior edge (dorsal and anal fin spines in juveniles are not available for study). This row of denticles gradually disappears in the larger, presumably adult individuals of *Lodeacanthus* (LDM 270/9, 38), except in the intermediate fin spines (Fig. 5.22). Also, similar denticles are observed on the pectoral spine only in juvenile individuals of *Acanthodes lopatini* (Beznosov, 2009). This condition is unknown for the juveniles of the other Acanthodiformes (Upeniece, in press).

### Scales and zones of squamation

**Scales.** The body is covered all over with the slanting rows of closely-spaced minute scales. The scales have an unornamented smooth rhomboidal-roundish crown and slightly constricted neck (Figs. 5.13, 5.14, 5.15). The microscopic pores are not seen. The crown has sharp posterior part which overlaps posteriorly placed scale (Fig. 5.14). Each scale is overlapped anteriorly and anterolaterally by adjacent scales.

The base is convex, its length is about 2/3 of crown length. The length of the scale bases in presumably adult individuals (total length about 4 cm) ranges from 0.065 mm on the tip of the caudal fin to 0.16 mm on the trunk region and on the head. The scale base is wider than it is long, except the hypochordal lobe and the tip of the axial lobe of the caudal fin, where become equal length and width.

Scales are increased in size by the addition of areal zones of growth to the crown throughout the ontogeny similar to what is known in *Acanthodes bridgei, A. lundi, A.* sp. (Zidek, 1985). There appears to be a definite correlation between the scale size and the overall specimen size.

**Scales of juveniles** differ from those of adults in having bases with a deep pit (Fig. 5.16). These scales cover the ventral surface of the acanthodian body, and are well seen in specimens LDM 270/12, 25, 36. The surrounding flank scales have flat bases, and on the dorsum the bases are conical. Scales with a deep pit occur also in the dorso-lateral part of the prepectoral region (LDM 270/12, 33) of juveniles, but they are broader. Noteworthty, specimen LDM 270/23 shows the extention of these scales (varying in size) on entire body, except the scaleless prepectoral region.

Supposedly, acanthodian fish first of all was covered by the scales of `juvenile` type and then by the scales with conical base of `adult` type. In adult individuals all the scales have more or less conical bases. Such scales are not observed in other acanthodians, possibly due to the absence of such small preserved individuals.

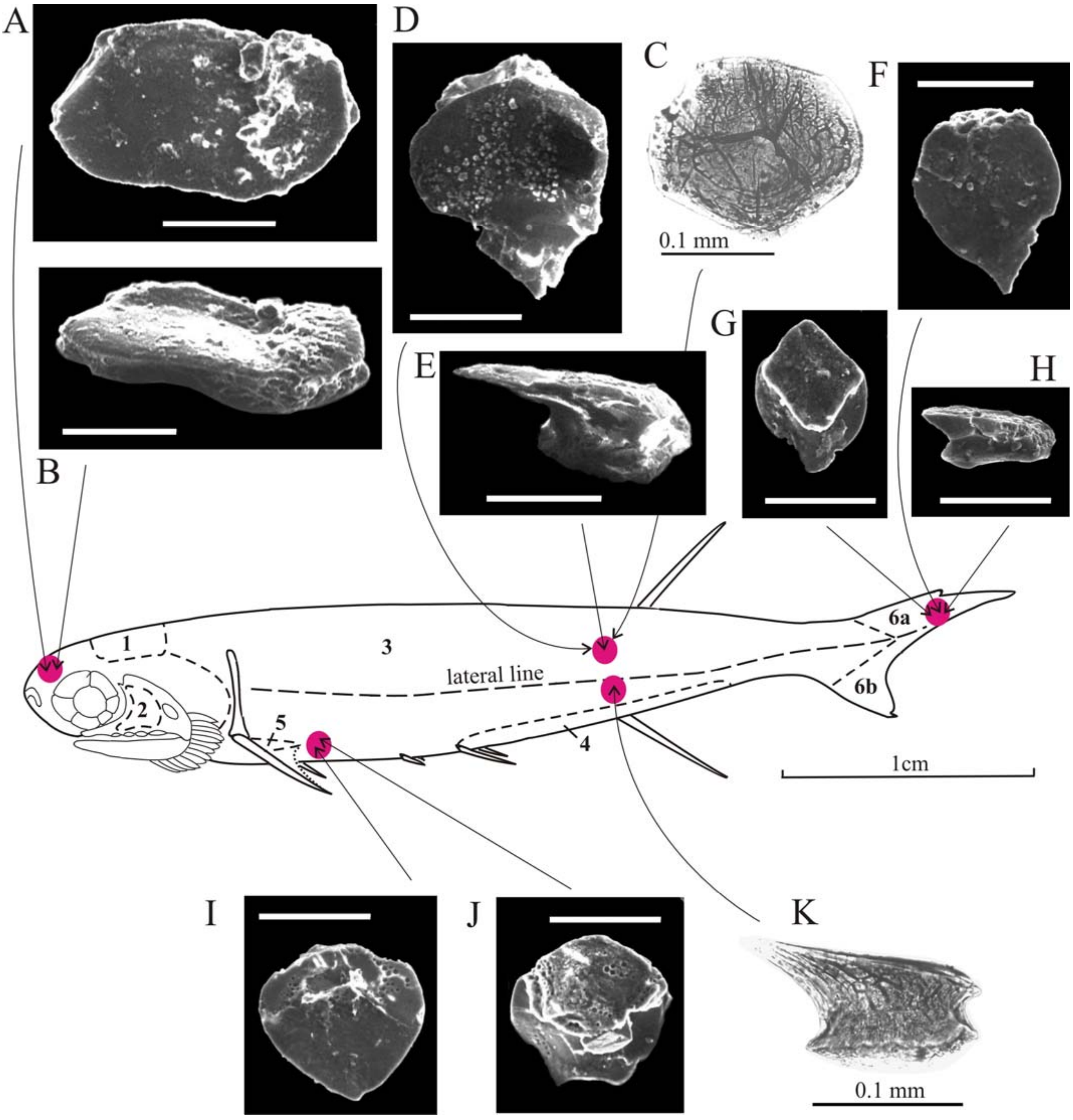


Fig. 5.13. Scales and tesserae of *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Fig. 1; Pl.1, figs.1-7; Pl. 2). Red circles indicate exact location of scales or tesserae. **A,B**, tesserae, specimen LDM 270/34c-1A; **C-E**, scales and section from the trunk zone, LDM 270/15a-2B; **F-H**, scales from the axial lobe, LDM 270/59-1c; **I,J**, scales from the trunk zone, LDM 270/55-1e; **K**, section of scale from the trunk zone, LDM 270/15a1B. Scale bar 0.1 mm.

5.13. att. Akantodes *Lodeacanthus gaujicus* zvīņas un tesēras (Upeniece, Beznosov, 2002, Fig. 1; Pl.1, figs.1-7; Pl. 2). Sarkanie aplīši ir to precīzas atrašanās vietas. **A,B**, tesēras, paraugs LDM 270/34c-1A; **C-E**, zvīņas un to plānslīpejumi no rumpja zonas, LDM 270/15a-2B; **F-H**, zvīņas no aksiālās daivas, LDM 270/59-1c; **I,J**, zvīņas no rumpja zonas, LDM 270/55-1e; **K**, zvīņas plānslīpējums no rumpja zonas, LDM 270/15a1B. Mēroga skala 0.1 mm.

*Triazeugacanthus* has relatively much larger scales and their bases are flat (Gagnier, pers.comm., Upeniece, 1996). According to Watson (1937), in *Mesacanthus mitchelli* "the scales measure about one-sixteenth of a millimetre across". So, the adult individuals of *Lodeacanthus* (Table 5.3) have much larger scales than *Mesacanthus.*

The **squamation** is almost completely developed in the individuals comprising 25 mm in total body length (Figs. 5.4, 5.14). The squamation consists of approximately 95-100 diagonal scale rows between the scapula and the caudal peduncle counted in adult individual (in holotype LDM 270/38). Rows of scales on the body flanks meet at an angle between 30-35 degrees.

Thirty adult and subadult individuals were used for research of the squamation, revealing the presence of several squamation zones of the body (Upeniece, Beznosov, 2002, Fig. 1). Six zones are distinguished based on the scale morphology and size (Fig. 5.13, 5.15): head and cheek zones, trunk (lateral) and ventral zones, caudal and pectoral fin zones. Several subzones can be marked in the trunk and caudal regions.

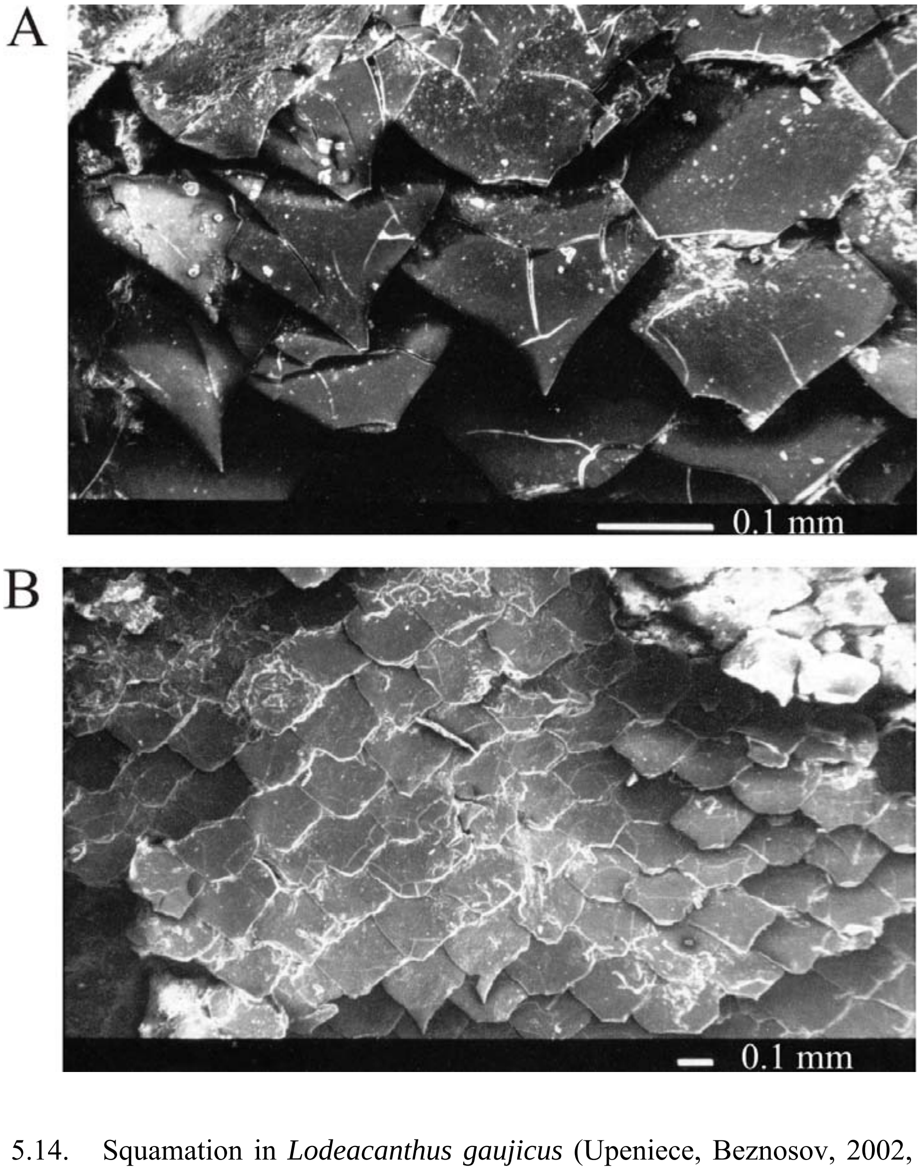


Fig. 5.14. Squamation in *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Pl. 1, figs. 8,9) of a trunk zone. **A,B**, specimen LDM 270/20. Scale bar 0.1 mm.

5.14. att. Akantodes *Lodeacanthus gaujicus* zvīņojums (Upeniece, Beznosov, 2002, Pl.1, Figs. 8,9) zvīņojums rumpja zonā. **A,B**, paraugs LDM 270/20. Mēroga skala 0.1 mm.

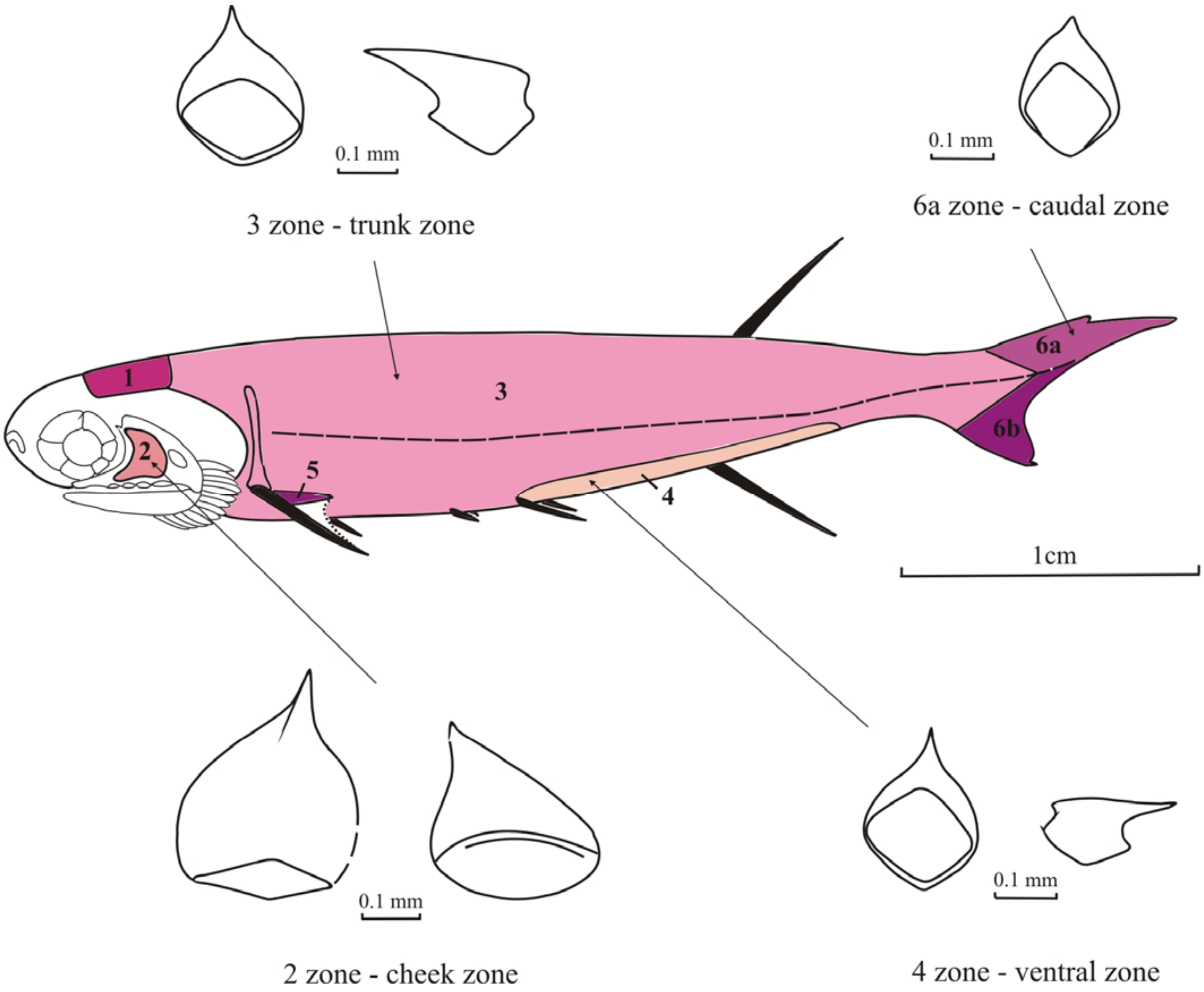


Fig. 5.15. Zones of squamation in acanthodian *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Fig. 1,2, with modifications). **1**, dorsal surface of the head; **2**, cheek region; scales from specimens LDM 270/9a, LDM 270/38a; **3**, trunk scales; scales from LDM 270/9, LDM 270/39; **4**, ventral scales; scales from LDM 270/9, LDM 270/7a; **5**, pectoral fin scales; **6**, caudal fin: **6 a**, scales of the axial lobe; scale from LDM 270/9; **6 b**, scales of the hypochordal lobe.

5.15. att. Akantodes *Lodeacanthus gaujicus* zvīņojuma zonas(Upeniece, Beznosov, 2002, Figs. 1, 2, ar izmaiņām). **1**, galvas dorsālā virsma; **2**, vaigu reģions; zvīņas no LDM 270/9a, LDM 270/38a; **3**, rumpja zvīņas; LDM 270/9, LDM 270/39; **4**, ventrālās zvīņas; LDM 270/9, LDM 270/7a; **5**, krūšu peldspuras zvīņas; **6**, astes peldspura: **6 a**, aksiālās daivas zvīņas; LDM 270/9; **6 b**, hipohordālās daivas zvīņas.

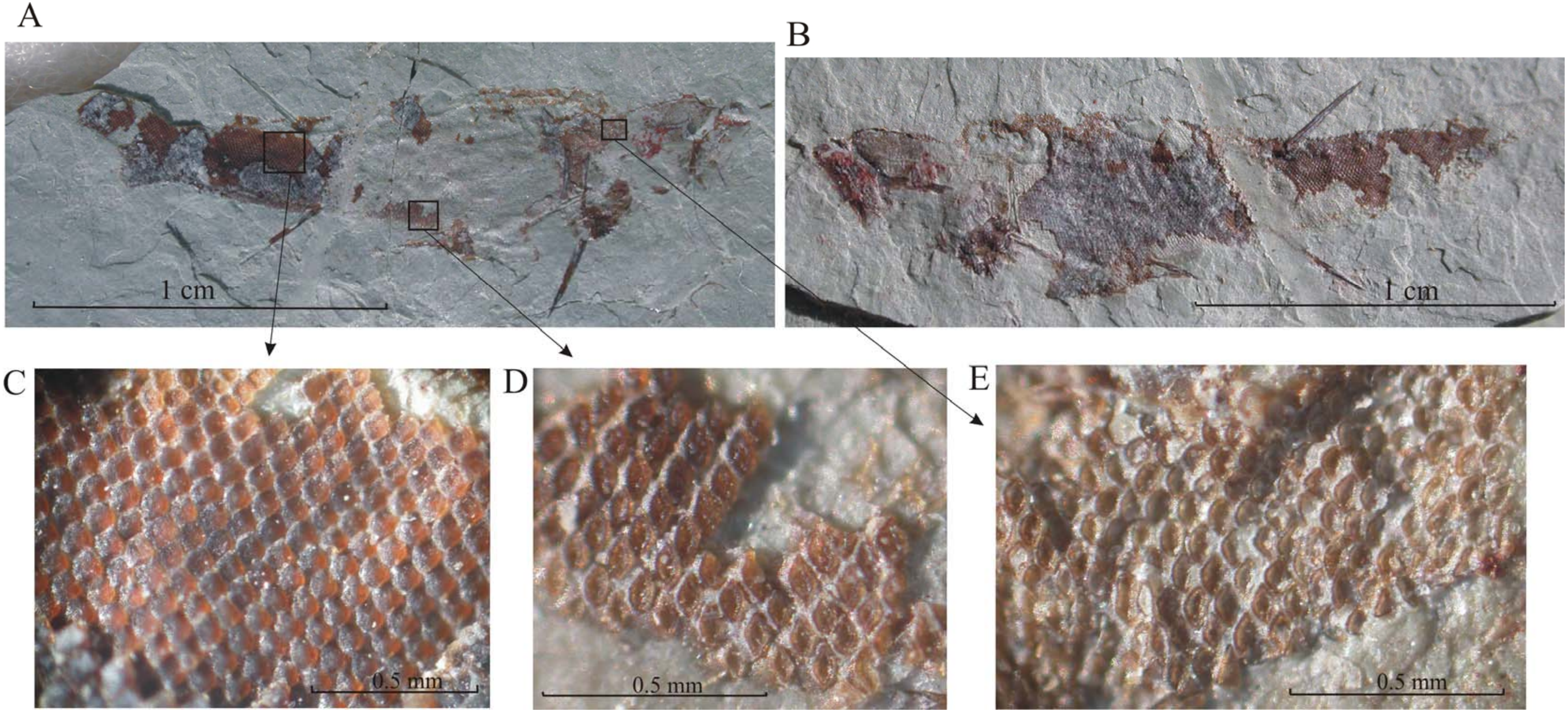


Fig. 5.16. Two types of base of the scale in juvenile individual of *Lodeacanthus gaujicus*. Specimen LDM 270/12. **A, B**, complete fish, counterpart and part; **C**-**E**, enlarged areas, marked by rectangular areas on A, showing conical bases of scales from lateral zone (C) (presumably fully developed); incompletely developed bases of scales with a deep ventral pit from the ventral (D) and dorso-lateral area (E) of prepectoral region.

5.16. att. Divu tipu zvīņu pamatnes akantodes mazulī *Lodeacantus gaujicus*. Paraugs LDM 270/12. **A, B**, vesels skelets, abas parauga pusītes; **C**-**E**, zvīņojuma palielinājumi; **C**, zvīņu koniskās pamatnes no sānu zonas (domājams, pilnībā attīstītas zvīnas); **D**, nepilnīgi attīstītas zvīņu pamatnes ar dziļu ventrālu iedobumu, vēdera zona; **E**, prepektorālā rajona zvīņas no muguras-sānu reģiona.

Squamation is present on the whole body except: 1) the narrow line on the ventral region between the pectoral fins, 2) the gill region, 3) the dorsal, pelvic, intermediate and anal fins. No clear traces are preserved on the fin membranes. Pectoral fins reveal only narrow zone (zone 5 in Fig.5.15) of squamation (specimens LDM 270/14, 26, 39).

The development of squamation during ontogeny begins from the posterior part of the body both in *Lodeacanthus* and *Acanthodes* (Upeniece, in press). The dorsal part of the body exhibits little faster scale covering during the ontogenesis of *Lodeacanthus*; the scales along the main lateral line do not considerably differ from the rest of the trunk scales. The squamation in *Acanthodes* first appears along the main lateral line; these scales are larger in size in comparison with the rest of the trunk scales that developed later. The development of squamation of the head starts along the sensory line both in *Lodeacanthus* and *A. bridgei* (Zidek, 1976) and *A. lopatini* (Beznosov, 2009).

The rates of squamation development differ considerably within *Acanthodes* species; the scale cover spread fastest in *A. lopatini*. In comparison, the mesacanthiid *Lodeacanthus* exhibits a considerably faster rate of squamation development than in other Acathodiformes.

The **head region** is most clearly distinguished having two zones of more enlarged scales and with low base, - on the dorsal surface (zone 1) and on the cheek region (zone 2, see Fig. 5.17). The scales of the cheek region have the largest crowns (their length is up to 0.39 mm) in the body squamation, exceeding their base up to five times (in the trunk zone only twice). The tesserae covering extends from between the orbits to the nasal region (Fig. 5.5 A,B).

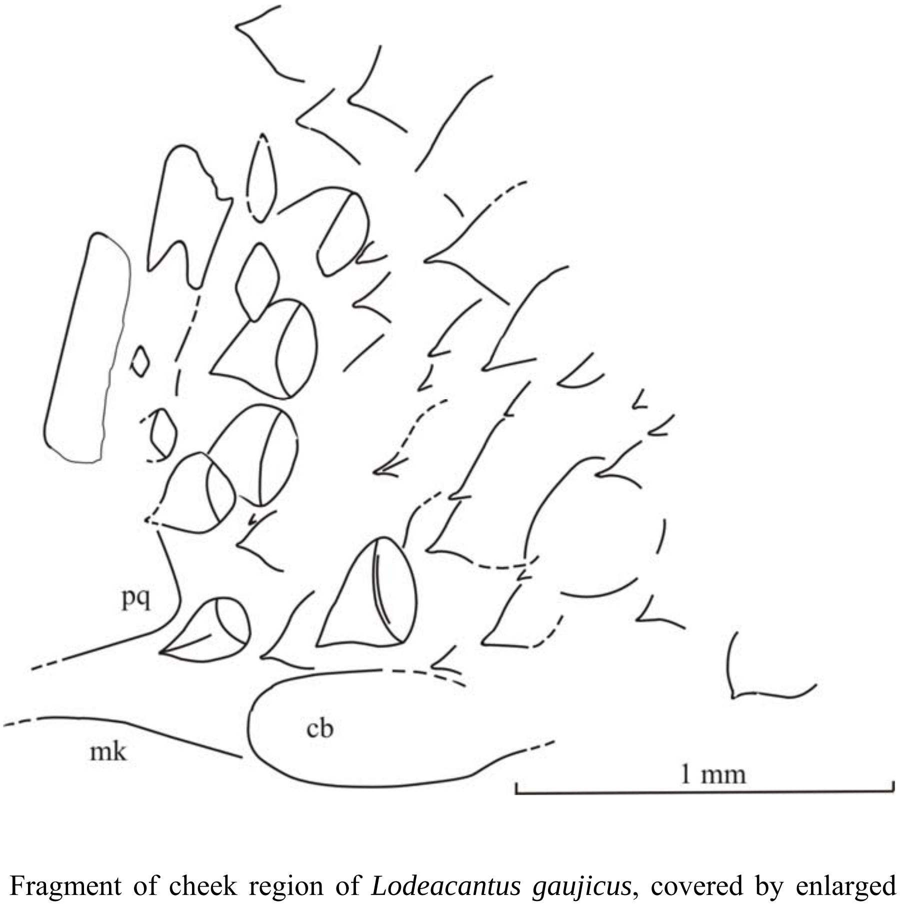
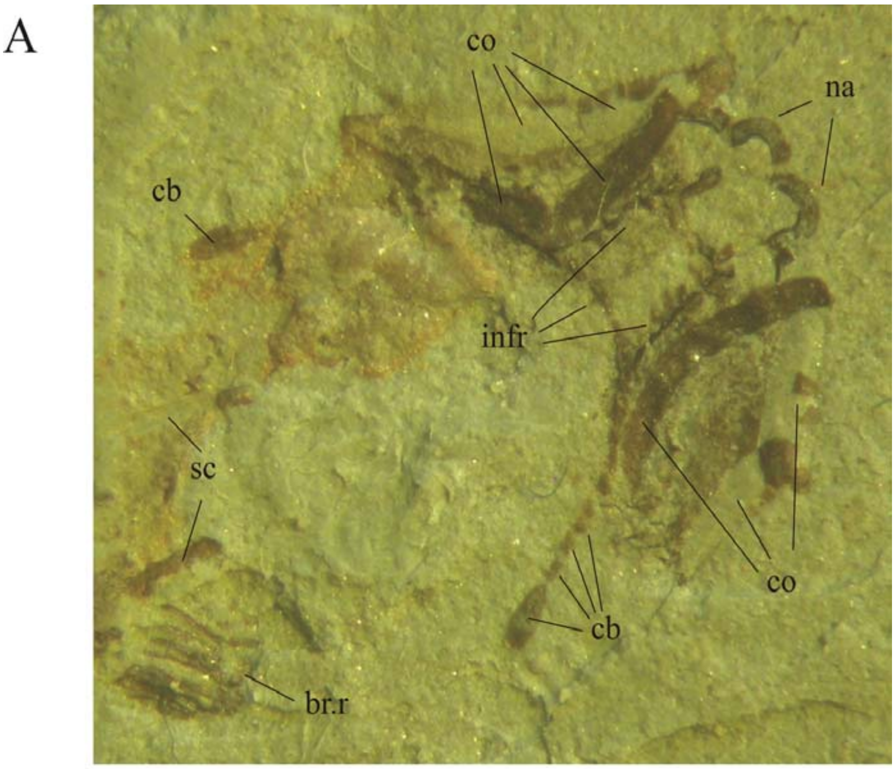


Fig. 5.17. Fragment of cheek region of *Lodeacantus gaujicus*, covered by enlarged scales (zone 2 in Fig. 5.15). Specimen LDM 270/38a.

5.17. att. Zvīņas uz akantodes *Lodeacantus gaujicus* galvas laterālā reģiona (sk. 2.zonu 5.15.att.). Paraugs LDM 270/38a.



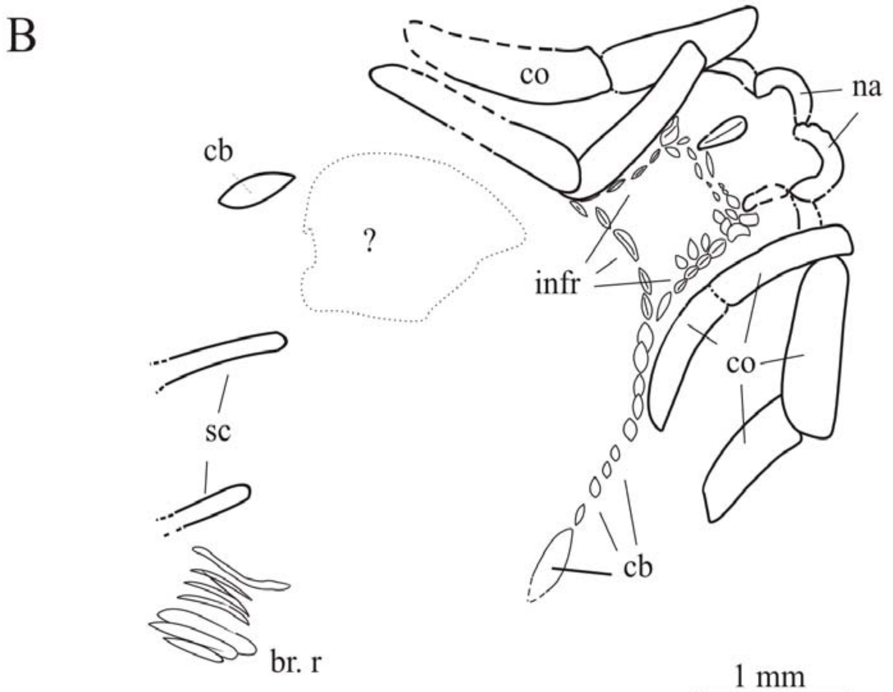


Fig. 5.18. Head of incompletely squamated individual of *Lodeacanthus* LDM 270/46. Infraorbital sensory line is visible. **A**, LDM 270/46b; **B**, combined drawing of a part (LDM 270/46a) and a counterpart (LDM 270/46b).

5.18. att. Ar zvīņojumu nepilnīgi segtas akantodes *Lodeacanthus gaujicus* galva LDM 270/46. Ir saglabājusies infraorbitālā sensorā līnija (infr). **A**, LDM 270/46b; **B**, kombinēts zīmējums pēc abām parauga pusītēm LDM 270/46a, LDM 270/46b.

**Trunk scales** (zone 3, Fig. 5.13, 5.15, 5.19) have a more pronounced bulging base, distinguishing them from all other scales of the body. The height of the scale comprises about 0.15 mm, the length of the crown – up to 0.27 mm; the length of the base is 0.14-0.17 mm, the width of the base is 0.17-0.23 mm.

The size of trunk scales diminishes downward from the main lateral line. The subzone, small area of some 20 rows of scales may be noted behind the scapula where the width of the scale bases becomes twice longer than their length (their ratio ranges between 0.43-0.59). The length of the bases of these scales is 0.09-0.14 mm, the width 0.16-0.27 mm. The size of these scales gradually diminishes in ventral direction. Dorsally, immediately behind the zone 1 a small area of somehow slightly smaller trunk scales appears, where a subzone may be traced. Similar zone of small scales is known in the occipital region of *Acanthodes lopatini* (Beznosov, 2000, zone A).

Smaller **ventral scales** are situated in the clearly distinguished region from the pelvic fins till some distance behind the anal fin and represents zone 4 (Fig. 5.15). The scale morphology is similar to that of the trunk scales (zone 3), and the length of the crown comprises about twice as the length of the scale base, too. The length of scale bases comprises 0.065-0.11 mm, gradually increasing till 0.15 mm in the bordering region with the lateral scales. The position of this zone is rather similar to that in *Poracanthodes menneri* (Valiukevičius, 1992).

The **fin scales** of the pectoral fin represents zone 5. The zone is narrow and gradually diminishes posteriorly; the length of the zone reaches nearly half of the fin length. Two subzones can be noted within this zone based on the difference in the scale size.

The scales of the **caudal fin** represents zone 6: 6a – the axial lobe, 6b – the hypochordal lobe. The scale morphology in these lobes differs in having a slightly different ratio between the length and the width of the scale bases (in 6a the ratio is 1.0, in 6b – 0.7-0.8). The bases are flat.

Generally the zonation of squamation and scale variability in *Lodeacanthus gaujicus* resembles that in *Acanthodes lopatini* (Beznosov, 2000).

### Sensory lines

The **main lateral line** is well seen (specimens LDM 270/12, 13, 22, 25, 38, 44) on the trunk (Figs. 5.6, 5.22) and is also well discernible in the tail region (Fig. 5.12 B). The scales bordering the main lateral sensory line do not differ in size and orientation from the rest of the flank scales. Holotype specimen LDM 270/38 reveals well marked interrupted line of red patches (Fig. 5.22 A) on the trunk above the main lateral line, – presumably remains of the vertebral column or the notochordal sheath.

Scales bearing the **infraorbital sensory line canal** are considerably different, and their bases are wedge-like (Fig. 5.6). These scales are well marked in incompletely squamated individuals (specimens LDM 270/3, 12). The infraorbital sensory line is best seen in dorso-ventrally preserved heads of specimens LDM 270/37, 46 (Fig. 5.18). The diameter of the infraorbital sensory line canal is 0.1 mm.

No traces of the **ventrolateral sensory line** have been found.

### 5.1.3. Histology of scales

The internal morphology of scales has been studied by two methods: in thin sections and using the aniseed oil. Small size and poor preservation of the scales in the most part of the squamation allowed to examine the histology only in the zone 3 (Figs. 5.13, 5.15, 5.19). Therefore a general description is given based on the trunk scales (Upeniece, Beznosov, 2002; Beznosov, Upeniece, 2002).

The histological structure corresponds to the *"Acanthodes"* – type (Fig. 5.19). The scale base is composed of acellular bone. Vascular canals are absent. The crown consists of mesodentine and is covered with relatively thin enameloid (?) layer. The system of dentine canals is well developed in the crown. The circular canals of the basal crown part are located accordingly to growth zones of the scale. They become thicker along the anterior edge and have several short branches. The ascending canals are better developed in the posterior part of the crown. They are represented by few relatively straight and thick main branches with smaller tubules. The latter often penetrate into the adjacent growth zones. The radial and primordial dentine canals are not seen. Scales increased in size by the addition of areal zones of growth to the crown both in *Lodeacanthus* (Upeniece, Beznosov, 2002) and in *A. bridgei* and *A. lundi* (Zidek, 1985).

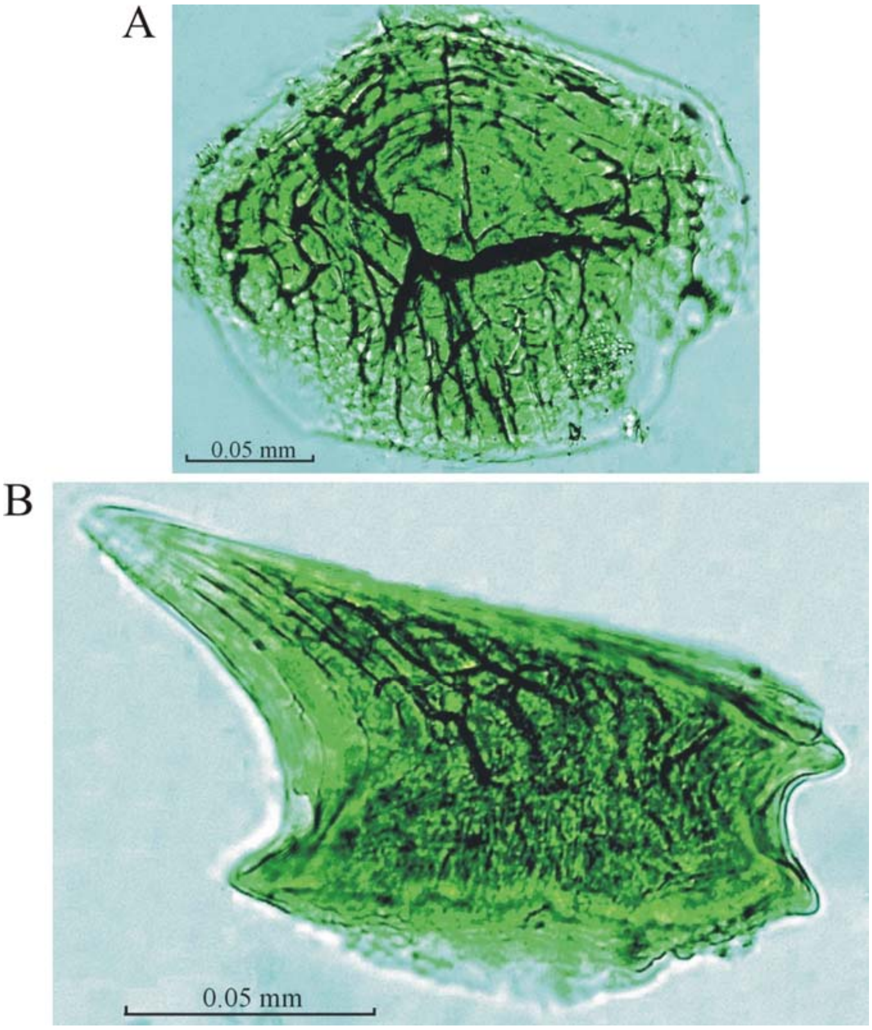


Fig. 5.19. Histology of scales of *Lodeacantus gaujicus* (Upeniece, Beznosov, 2002, Plate 2). Scale of trunk zone. **A**, horizontal section through the crown, specimen LDM 270/15a-2B; **B**, vertical longitudinal section, LDM 270/15a-1B.

5.19. att. (iepr.lpp.) Akantodes *Lodeacantus gaujicus* zvīņu plānslīpējumi (Upeniece, Beznosov, 2002, Plate 2). **A**, zvīņas kronas horizontālais plānslīpējums, LDM 270/15a-2B; B, zvīņas vertikālais plānslīpējums, LDM 270/15a-1B.

### 5.1.4. Comparison of *Lodeacanthus* with related genera

*Lodeacanthus* is a member of the Mesacanthidae retaining a pair of intermediate spines; fin spines are inserted superficially, and scales cover the entire body. *Lodeacanthus* is evidently more closely related to *Triazeugacanthus* than to *Mesacanthus.* Some features are similar to *Triazeugacanthus* (lower jaw without mandibular splint, the ratio of fin spines), some to *Mesacanthus* (the same ornamentation of fin spines, the presence of a small epichordal lobe), some are 'between' these genera: the branchiostegal rays are longer and more numerous than in *Triazeugacanthus,* but are shorter than in *Mesacanthus; Lodeacanthus* has comparatively smaller body scales than in *Triazeugacanthus,* but considerably larger than in *Mesacanthus. Lodeacanthus* possess some unidentified small bones located on the posterior margin of the palatoquadrate.

***Lodeacanthus* differs from *Triazeugacanthus*** in many aspects:

- the presence of a pair of nasal bones in *Lodeacanthus* (in *Mesacanthus* it is unknown),
- the ornamentation of circumorbitals is concentric in *Lodeacanthus* and pitted in *Triazeugacanthus*,
- the ornamentation of fin spines and the shape of the section of fin spines,
- presence of the epichordal lobe,
- all the scales have conical bases (in *Triazeugacanthus* they have flat bases),
- intermediate spines are twice longer than in *Triazeugacanthus*.

**Differences from *Mesacanthus*** are:

- in *Lodeacanthus* the jaws are ossified as a single unit (in *Mesacanthus* the jaws are ossified from to units; in *Triazeugacanthus* it is unknown),
- in *Lodeacanthus* a mandibular splint is absent,
- in *Lodeacanthus* subsidiary gill covers are absent,
- in *Lodeacanthus* the palatoquadratum is fenestrated (in *Triazeugacanthus* it is unknown).

*Lodeacanthus* differs from both related genera *Triazeugacanthus* and *Mesacanthus* by the presence of dermal bones of the cheek region, a pair of nasal bones, and of scale covering on the base of the pectoral fins.

## 5.2. Ontogeny of *Lodeacanthus gaujicus*

### 5.2.1. Development of squamation

All developmental stages from juveniles without scale covering to fully scaled specimens are known (Fig. 5.4). About one fourth of about sixty specimens are juveniles with an incomplete development of squamation or they represent merely a film of the skin with fin spines and head elements (Upeniece 1996, 2001a, 2005b, 2011). Juvenile individuals are covered partly by a film of skin and partly by scales (Figs. 5.4, 5.20, 5.21). Scales of juveniles differ from those of adults in having bases with a deep pit as mentioned earlier (Fig. 5.16).

The squamation develops more rapidly in the dorsal part of the body (Figs. 5.4, 5.6, 5.21). The scale cover spreads diagonally forward from the tail (Fig. 5.23), unlike to modern fishes. Fully scaled individuals reveal the presence of all six squamation zones of the body (Fig. 5.15).

The rate of development of the squamation is of interest (Table 5.3, Fig. 5.4). The squamation is nearly fully developed in 25.0 mm long specimens (LDM 270/37). In specimen LDM 270/28, whose estimated total length is 13.6 mm (Fig. 5.20), the scale cover reaches forward to the dorsal spine, and squamation extent is approximately 37% of the total body length. There are significant changes in the rate of the squamation extent when juvenile reaches about 20 mm in it total length: it boom from 54% to about 80%.

Three stages of the ontogenetic development (Fig. 5.23) are defined for the *Lodeacanthus gaujicus* in conjunction with development rate of the squamation:

**1 stage. Without the squamation** (Figs. 5.2, 5.23 A)

The body is covered merely with a film of the skin; the head is indicated only by the presence of an eye stain, as well as by a few branchiostegal rays (Upeniece, 2001 a, Col.-Pl.2, Fig.10). Well developed fin spines and scapula are present. The estimated length of the body is about 8 mm (Fig. 5.4: LDM 270/45), and it comprises the smallest whole-bodied acanthodian ever found in the fossil record.

**2 stage. Incompletely developed squamation** (Figs. 5.6, 5.20, 5.21).

Three substages are recognized:

a) Initial stage of the scale covering of the body reaches the dorsal and the anal fin spine (Figs. 5.20, 5.23B); the squamation extent is about 37% of the total body length. This ontogenetic substage includes newly ossified four circumorbital bones of about similar length, a pair of nasal and cheek bones, as well as the remains of the endocranium. The estimated total length of the body is 13.6 mm (Fig. 5.4: LDM 270/28).

b) Squamation reaches diagonally forward to the level of the pelvic fin spines (Figs. 5.21, 5.23 C) on the dorsal side and to the anal fin spine on the ventral part. Squamation extent is 54% of the total body length. The main lateral line on the body appears in this substage. Specimens, representing this ontogenetic substage, are incompletely preserved to estimate the total length of the body (Fig. 5.4: LDM 270/1, 270/25, 270/44).

Table 5.3. The development of the squamation extent in acanthodian *Lodeacanthus gaujicus* (Upeniece, 1996, Table 2, with modifications)

5.3. tabula. Zvīņojuma attīstība akantodēs *Lodeacanthus gaujicus* (Upeniece, 1996, Table 2, ar izmaiņām)

| Stage of ontogeny | Specimen | Total length of body, mm | Prepectoral length, mm | Distance from pect. spine to end, mm | Pectoral – dorsal spine distance, mm | Squamation extent, mm | Squamation extent (% of total length) | Anterior squamation reach | Scales per mm in a row * |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 270/ 45 | (~ 8.0) | 2.65 | - | 2.9 | 0 | 0 | absence of squamation | 0 |
| 2 a | 270/ 28 | (~13.6) | 3.8 | - | ~ 4.7 | (~5.1) | 37 | dorsal spine | 16 |
| 2 b | 270/ 44 | - | - | - | 6.1 |  |  | pelvic spine | 16 |
|  | 270/ 1 | - | - | - | (7.2) |  |  | pelvic spine | 16 |
|  | 270/ 25 | (~19.6) | (~5.5) | 14.1 | 8.0 | ~10.6 | 54 | pelvic spine | 14 |
| 2 c | 270/ 23 | ~ 20.6 | ~5.5 | 15.1 | ~ 8.9 | 16.4 | 80 | ventral part of prepectoral region | 12.5 |
|  | 270/ 22 | 20.5 | 5.5 | 15.0 | 6.8 | 16.6 | 81 | endocranium | 11 |
|  | 270/ 3 | ~ 20.8 | 5.5 | ~15.3 | 7.5 | 17.0 | 82 | endocranium | 11 |
|  | 270/ 12 | 23.0 | 5.5 | 17.5 | 8.6 | 19.4 | 84 | endocranium | 10 |
| 3 | 270/ 37 | 25.0 | 6.4 | 18.6 | - | 25.0 | 100 | entire body | 10 |
|  | 270/ 2 | - | 8.3 | - | - |  | 100 | — " — | 7.5 |
|  | 270/ 19 | ~34.7 | 8.7 | 26.0 | 13.0 | ~34.7 | 100 | — " — | 7 |
|  | 270/ 38 | 37.6 | 8.8 | 28.8 | 14.3 | 37.6 | 100 | — " — | 6 |
|  | 270/ 41 | 38.3 | ~7.5 | 30.8 | 14.7 | 38.3 | 100 | — " — | 6 |
|  | 270/ 9 | 38.9 | ~8.4 | 31.0 | 16.0 | 39.4 | 100 | — " — | 7 |

* Scales measured between the dorsal spine and caudal peduncle (see also Fig. 5.3. for distance explanations).
Values in parentheses means the estimated specimen total length unlike the measured values.

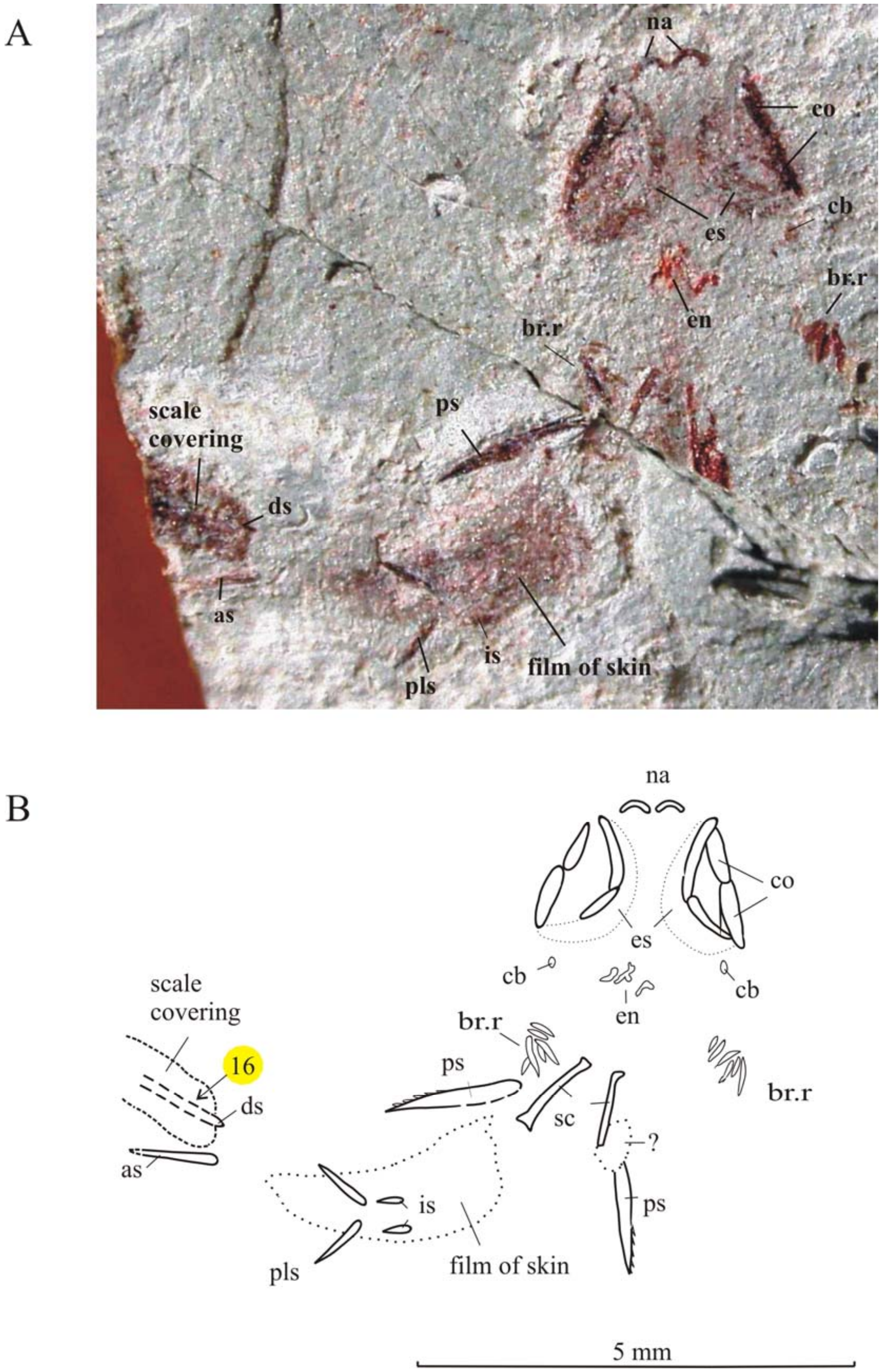


Fig. 5.20. Juvenile individual of *Lodeacanthus gaujicus* LDM 270/28. Squamation reaches the dorsal fin spine (ds). Film of skin covers the middle part of the trunk (Upeniece, 1996, Fig. 2 B). 16, number of scales per millimeter in a row. **A**, photo. **B**, drawing of the same specimen.

5.20. att. Akantodes *Lodeacanthus gaujicus* mazulis LDM 270/28. Zvīņojums attīstījies līdz dorsālās peldspuras dzelksnim (ds). Ķermeņa vidusdaļā ir saglabājušās ādas pigmentējuma atliekas (Upeniece, 1996, Fig. 2 B). 16 – zvīņu skaits vienā milimetrā. **A**, foto. **B**, zīmējums pēc tā paša parauga.

c) Squamation reaches diagonally forward to the level of the pectoral fin spines (Figs. 5.6, 5.23 D); squamation extent reaches 80-84% of the total body length. The isolated patch of squamation covers the area of the ventral part of the prepectoral region (between pectoral fin spines). Then the posterior part of the prepectoral region became squamated. The only scales of the head are represented by the two rows along the infraorbital sensory line, which must be marked as newly appeared skeletal element (LDM 270/12). Simultaneously the tesserae covering had been spread to between the orbits. A row of small cheek bones is present (Figs. 5.6, 5.18).

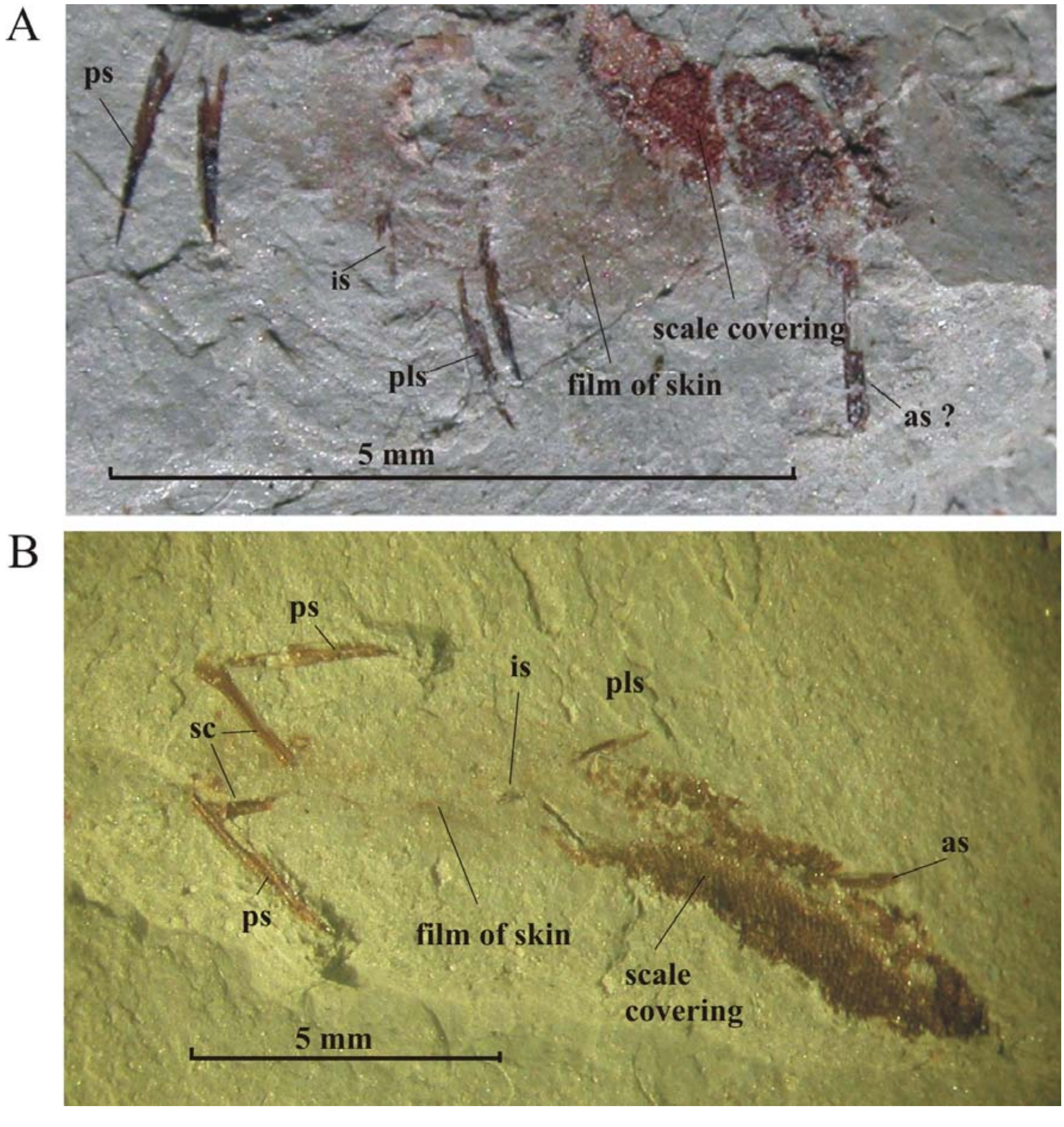


Fig. 5.21. Incompletely developed squamation of juvenile individuals of *Lodeacanthus gaujicus*. Squamation reaches diagonally forward to the level of the pelvic fin spines. The rest of the trunk is covered by the film of skin. Caudal part is to the right. A, specimen LDM 270/1 b; B, LDM 270/44 a.

5.21. att. Akantožu *Lodeacanthus gaujicus* mazuļi ar nepilnīgi attīstītu zvīņojumu. Zvīņojums stiepjas diagonāli uz priekšu līdz iegurņa peldspuru dzelkšņu līmenim. Pārējo ķermeņa daļu iekontūrē saglabājies ķermeņa ādas pigmentējums. A, paraugs LDM 270/1 b; B, LDM 270/44 a.

Circumorbital bones have increased in number up to five by adding of a small bone (LDM 270/22). Behind the pelvic fin spines the small unscaled region retains in the ventral area covered by the film of skin. The total length of the body in this ontogenetic substage ranges from 20.6 to 23.0 mm (Fig. 5.4: LDM 270/23, 270/22, 270/3, 270/12).

**3 stage. Fully developed squamation** (Figs. 5.1, 5.18, 5.22, 5.23E).

The Meckelian cartilage, palatoquadrate and branchial arches become ossified only after the scale covering of the body and the head is complete. From this ontogenetic stage the acanthodian individuals are considered to be adults although they continue growing. The cheek area is covered by enlarged scales (Fig. 5.17). The circumorbital ring consists of presumably six elements (Fig. 5.7), unlike what is observed in juvenile individuals. The small pectoral fin (Fig. 5.15, zone 5) is marked by very minute scale covering. The total length of the body in that ontogenetic stage ranges from 25.0 to about 48.2 mm (Fig. 5.4: LDM 270/37, 270/19, 270/38, 270/41, 270/9; Table 5.5).

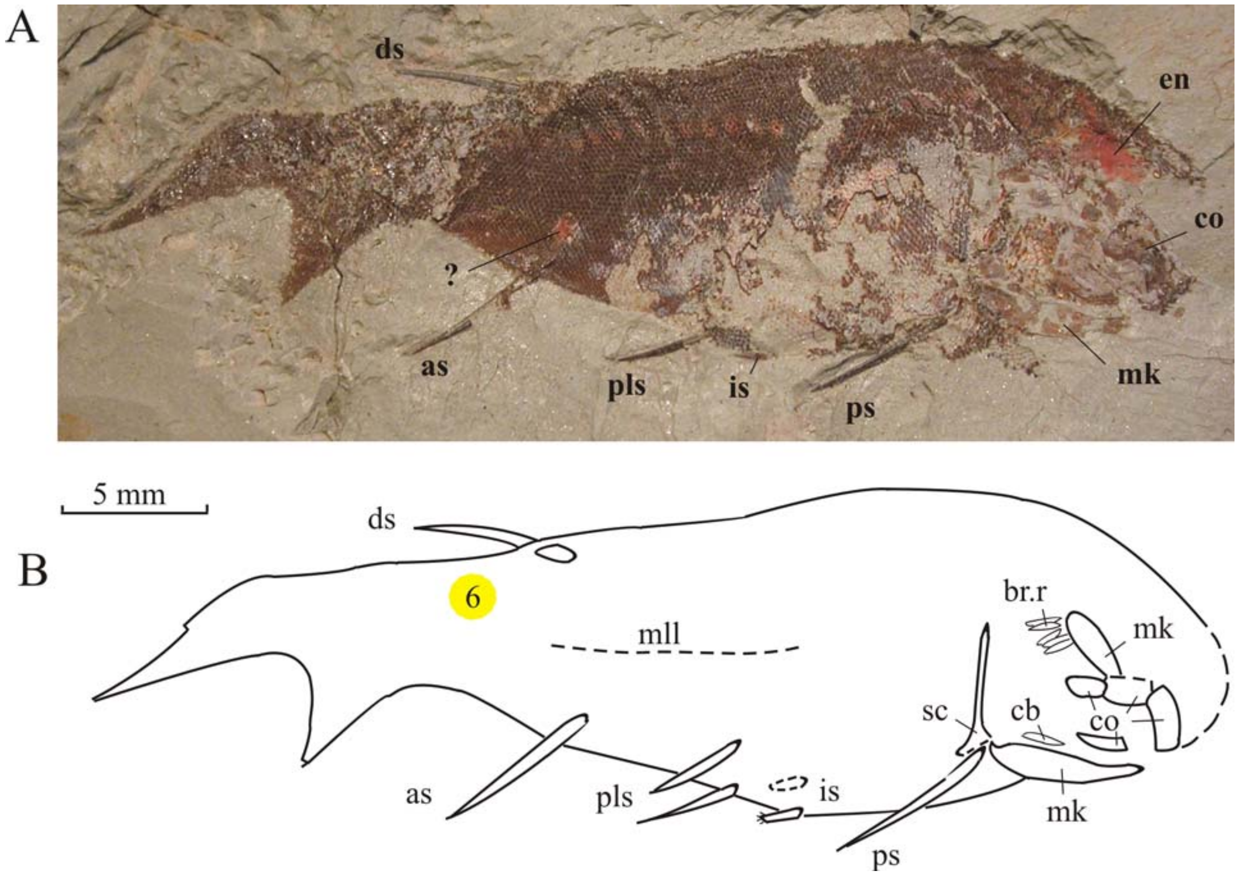


Fig. 5.22. Presumably adult individual of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1 A), see also the squamation extent in Fig. 5.4. Holotype LDM 270/38. **A**, photo of LDM 270/38a. **B**, drawing of a part and counterpart: LDM 270/38a, LDM 270/38b.

5.22. att. Akantodes *Lodeacanthus gaujicus*, domājams, pieaudzis indivīds (Upeniece, 1996, Fig. 1 A), skatīt arī zvīņojuma attīstības pakāpi 5.4. att. Holotips LDM 270/38. **A**, LDM 270/38a; **B**, zīmējums pēc abām parauga pusītēm: LDM 270/38a un LDM 270/38b.

**Other known ranges of acanthodian juveniles** comes from *Acanthodes gracilis* (Zajic, 2005), *A. bronni*, (Heidtke, 1990), *A.bridgei*, *Howittacanthus kentoni* (Zidek, 1988) and *A.lopatini* (Obruchew, 1955, fig.7.; Novitskaya, Obruchew, 1964, Pl. I, Fig. 8; Beznosov, 2009). In all acanthodians the development of the squamation extent starts from the caudal part (Fig. 5.24). In Acanthodidae the squamation develops first along the main lateral sensory line, but in Mesacanthidae (*Lodeacanthus*) – bias to the body - along the diagonal located rows of the scales. Only in the head of *Lodeacanthus* the squamation develops along the infraorbital sensory line similar to that in *Acanthodes bridgei* (Fig. 5.24 A,C).

Zidek (1976) noted for North American Pennsylvanian *Acanthodes* that most of the squamation formed before the fish reached approximately 50% of their maximum length (410 mm). In *Lodeacanthus* the squamation is fully developed in specimen 25.0 mm long (Fig. 5.4, LDM 270/37). Therefore it can be concluded that the fish became fully scaled fairly early in its ontogeny (Zidek, 1976) and it could have mean that the entire body length of mature individuals of *Lodeacanthus* would be about 50 mm. The largest known *Lodeacanthus* reaches 48.25 mm in estimated total body length (LDM 270/10). Although it is about eight to nine times smaller than the above mentioned largest *Acanthodes* (Fig. 5.24), it possibly could have been used for acanthodians` comparison.

### 5.2.2. Sequence of ossification of skeletal elements

The sequence of ossification (Table 5.4) has been reconstructed after the investigation of the ontogenetic stages of the *Lodeacanthus*. The first skeletal elements to ossify in the smallest juvenile individual with undeveloped squamation extent at all (Fig. 5.2) were endoskeletal scapula, exoskeletal branchiostegal rays and fin spines, then followed by endocranium, and exoskeletal head bones: circumorbital, nasal and cheek bones in little larger juvenile with squamation extent of 37% of the total body length (Fig. 5.20).

Sensory lines become visible slightly later in ontogeny, starting with the main lateral line (squamation extent of 54%) and following by the infraorbital sensory line (81%, respectively). Then tesserae became ossified at squamation extent of 84%. Jaws (Figs. 5.8, 5.22) and branchial arches (Fig. 5.10) become ossified only after squamation extent is completely developed.

The sequence of ossification of bones during the ontogeny is similar both in *Lodeacanthus* and *Acanthodes* (Upeniece, in press). No otoliths are visible in *Lodeacanthus*, which are well observed in *Acanthodes* (Heidtke, 1990, figs. 10-12; Zajic, 2005, figs. 39, 40; Beznosov, 2009, fig. 4 D).

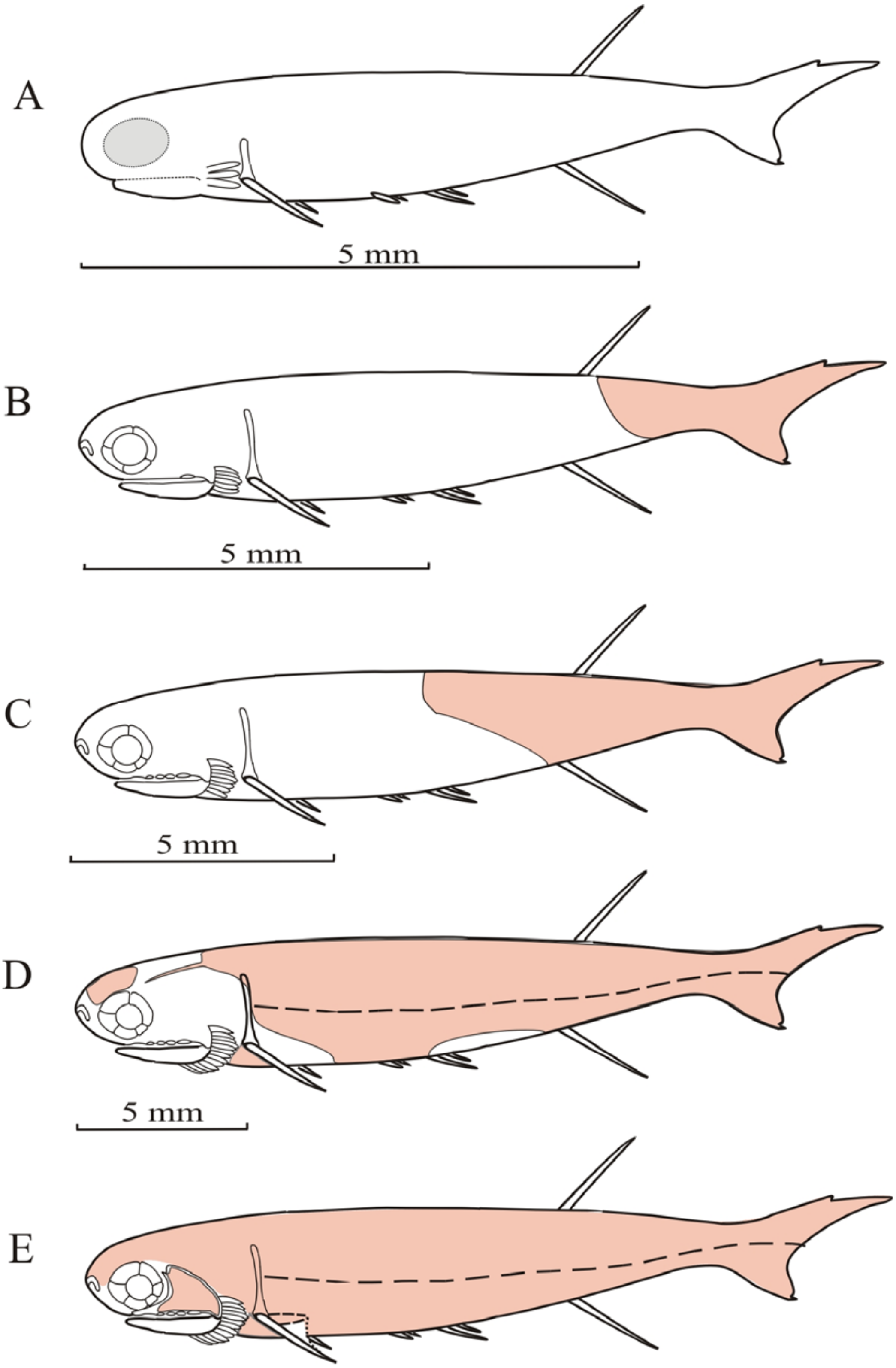


Fig. 5.23. Sequence of development of the squamation and head elements in *Lodeacanthus gaujicus*. **A**, stage of development without squamation; **B-D**, incompletely developed squamation; **E**, completely developed squamation.

5.23. att. Zvīņojuma un galvas elementu attīstības secība akantodei *Lodeacanthus gaujicus* **A**, bez zvīņojuma seguma; **B-D**, nepilnīgi attīstījies zvīņojums; **E**, pilnīgi attīstīts zvīņojums.

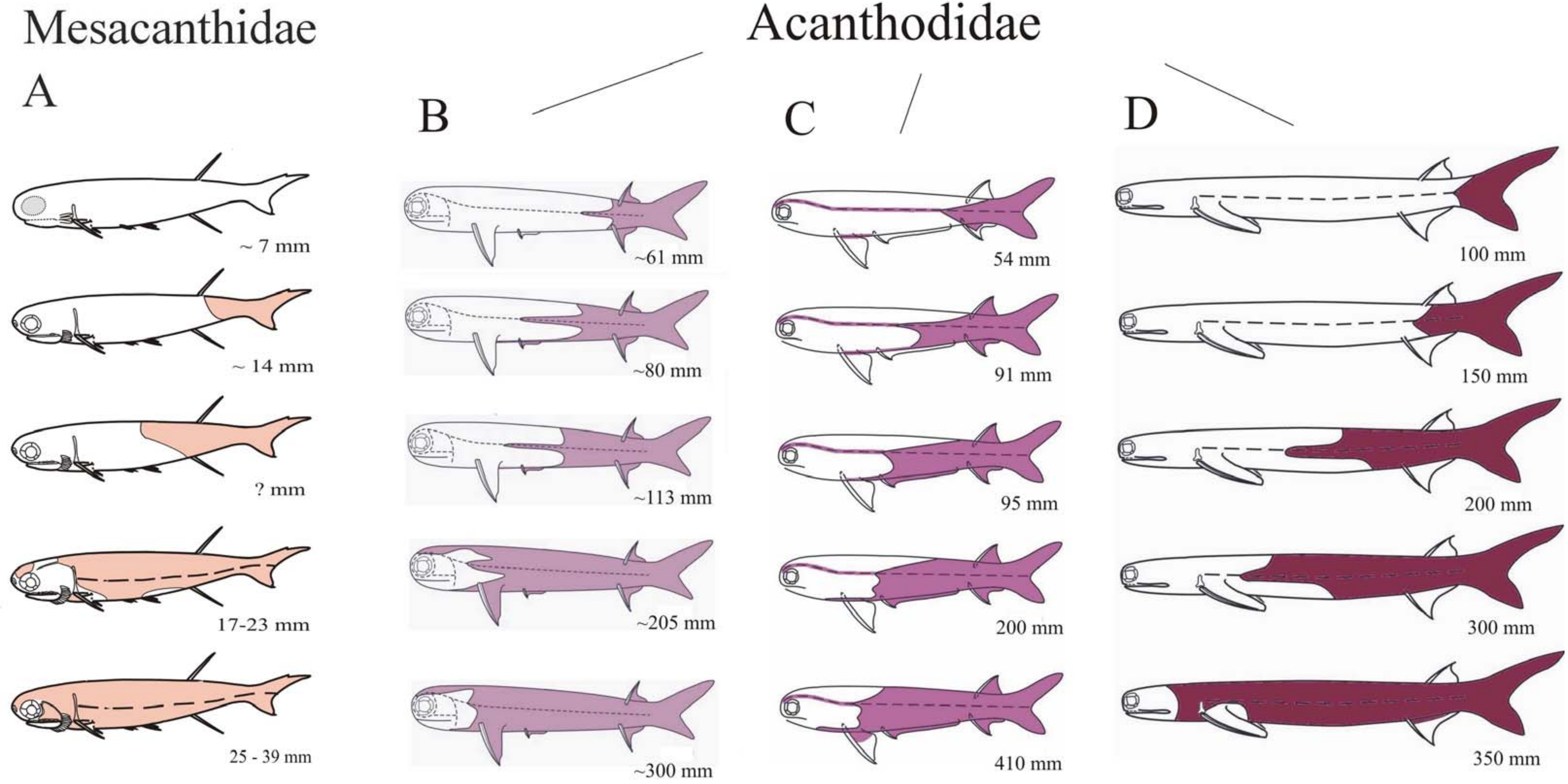


Fig. 5.24. Comparison of development of the squamation in Mesacanthidae **(A)** and Acanthodidae **(B-D)**: **A**, *Lodeacanthus gaujicus* Upeniece (Upeniece, 2011a); **B**, *Acanthodes gracilis* Beyrich (Zajic, 2005, Fig. 23); **C**, *Acanthodes bridgei* Zidek (Zidek, 1976, Fig. 13); **D**, *Acanthodes bronni* Agassiz (Heidtke, 1990, Fig. 52).

5.24. att. Zvīņojuma attīstības salīdzinājums Mesacanthidae **(A)** un Acanthodidae **(B-D)** dzimtām: **A**, *Lodeacanthus gaujicus* Upeniece (Upeniece, 2011 a); **B**, *Acanthodes gracilis* Beyrich (Zajic, 2005, Fig. 23); **C**, *Acanthodes bridgei* Zidek (Zidek, 1976, Fig. 13); **D**, *Acanthodes bronni* Agassiz (Heidtke, 1990, Fig. 52).

Table 5.4. Sequence of ossification (in red) of skeletal elements in juveniles and adults of *Lodeacanthus gaujicus*
5.4. tabula. Kaulu pārkaulošanās secība (sarkanā krāsā) akantožu *Lodeacanthus gaujicus* mazuļos un pieaugušajos īpatņos

| Onto-genetic stage | Speci-men | Length of body, mm | Prepec-toral length, mm | **Endoskeleton** | | | | **Exoskeleton** | | | | | Sensory lines | | Squamation extent (% of total length) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | sca-pula | endocra-nium | jaws | branch. arches | branch. rays | circum-orb. bones | nasal bones | cheek bones | tesser-rae | trunk | head | |
| 1 | 270/ 45 | (~8.0) | 2.65 | 🟥 + | ? | - | - | 🟥 + | - | - | - | - | - | - | 0 |
| 2 a | 270/ 28 | (~13.6) | 3.8 | + | 🟥 + | - | - | + | 🟥 + | 🟥 + | 🟥 + | - | n | - | 37 |
| 2 b | 270/ 25 | (~19.6) | - | n | n | n | n | + | n | n | n | n | 🟥 + | n | 54 |
| 2 c | 270/ 22 | ~20.5 | 5.5 | + | + | - | - | + | + | + | + | - | + | 🟥 + | 81 |
| | 270/ 23 | ~20.6 | ~5.5 | + | n | - | - | + | + | n | + | ? | + | + | 80 |
| | 270/ 3 | ~20.8 | 5.5 | + | + | - | - | + | + | n | + | ? | + | + | 82 |
| | 270/ 12 | 23.0 | 5.5 | + | + | - | ? | + | + | + | + | 🟥 + | + | + | 84 |
| 3 | 270/ 37 | 25.0 | 6.4 | + | + | 🟥 + | n | + | + | + | n | + | + | + | 100 |
| | 270/ 2 | - | 8.3 | + | + | + | 🟥 + | + | + | + | n | + | n | n | 100 |
| | 270/ 19 | ~34.7 | 8.7 | + | n | + | n | + | + | + | + | + | n | n | 100 |
| | 270/ 38 | ~37.6 | 8.8 | + | + | + | n | + | + | n | + | + | + | n | 100 |
| | 270/ 41 | 38.3 | ~7.5 | + | + | + | n | + | + | + | + | + | n | n | 100 |
| | 270/ 9 | 38.9 | ~8.4 | + | + | + | n | + | n | n | + | n | n | n | 100 |
| | 270/ 14 | - | ~9.0 | + | + | + | + | + | + | n | n | + | n | n | 100 |

🟥 + first appearance of skeletal element,
\+ presence of skeletal element,
\- absence of skeletal element,
n particular part of fossil is not preserved,
? skeletal element possibly could be present.
Values in paretnheses show the estimated total specimen length unlike the measured values.

### 5.2.3. Changes of proportions of body

The significant changes of proportions of the body during ontogeny can be seen in the ratio of the prepectoral distance (head plus gill region) to the total length of the body: in juvenile unsquamated individuals it comprises 33 %, decreasing to about 25 % in nearly squamated ones, and up to 20 % in adults (Fig. 5.25.). Remarkably changes of trunk proportions can not be stated.

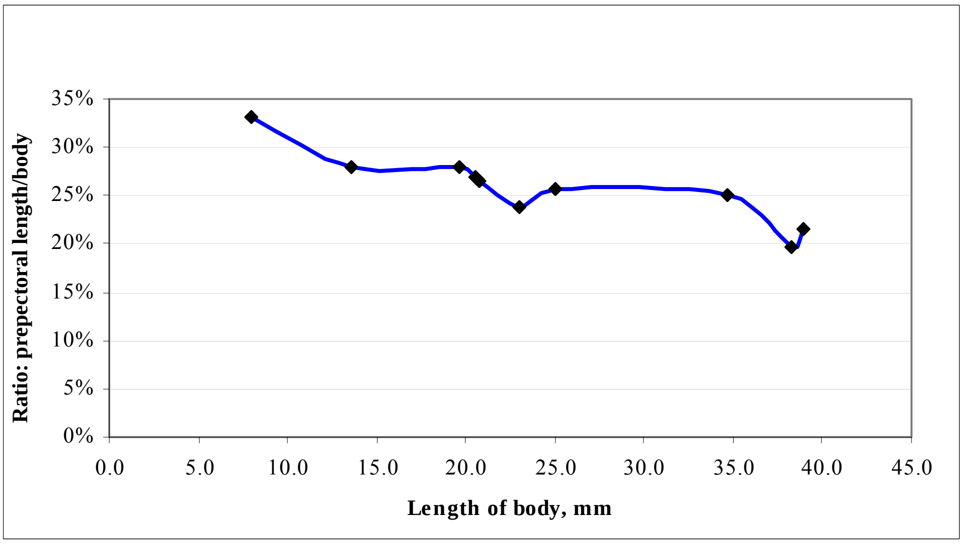


Fig. 5.25. Changes of proportions between the prepectoral distance and the total length of the body during the growth.

5.25. att. Proporciju izmaiņas starp prepektorālo garumu un ķermeņa kopgarumu augšanas laikā.

The fin spines could have been the less deformed elements and therefore are most useable for the determination of the agedness. There are remarkable changes during the ontogeny regarding the proportions of the length of the fin spines (Fig. 5.26): 1) ratio between the intermediate (is) and anal fin spine (as) increases from 17 to 27% (A); 2) ratio between the intermediate and pectoral fin spine (ps) increases from 15 to 28% (B); 3) ratio between the pelvic (pls) and pectoral fin spine increases from 38 to 63% (C); 4) ratio between the pelvic and anal fin spine increases from 42 to about 60% (D); 5) but the ratio between the intermediate and pelvic fin spine is variable: it fluctuates between 31-53%.

The pectoral, anal and dorsal fin spines of each individual are of the equal length. Therefore the ratio between them remains constant during the growth, as well as between the intermediate and pelvic spines. Mentioned fin spines are reflecting two groups with differently marked rate of development. In the earlier ontogenetic stages the intermediate and pelvic fin spines (represent the first group: spines are small and flat) are proportionally smaller than anal, dorsal and pectoral spines (represent the second group: spines are long and stout). This proportion gradually slightly had been changed during the ontogeny.

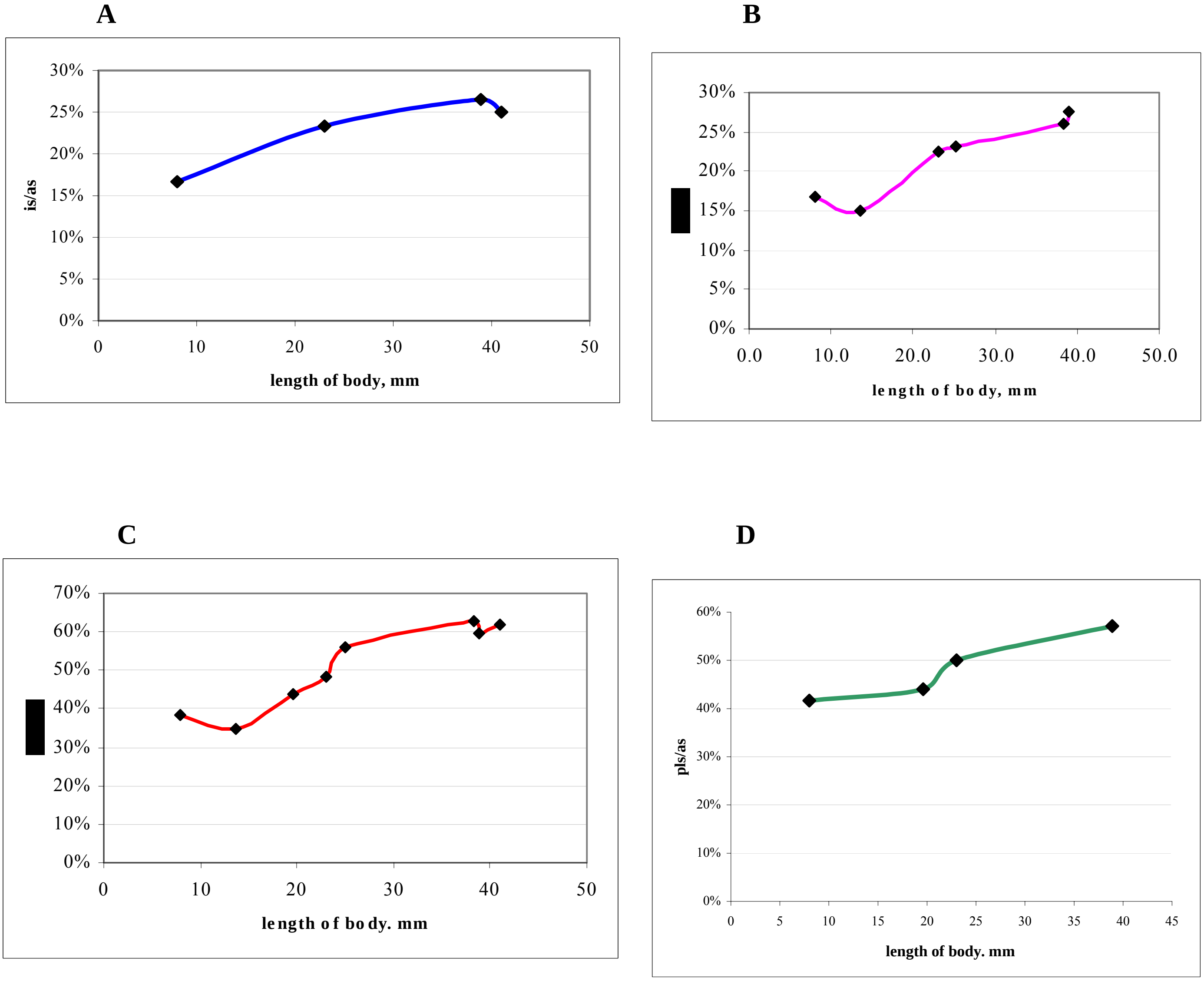


Fig. 5.26. Changes of proportions of fin spines during the growth. **A**, between the intermediate and anal fin spine; **B**, between the intermediate and pectoral fin spine; **C**, between the pelvic and pectoral fin spine; **D**, between the pelvic and anal fin spine.

5.26. att. Peldspuru dzelkšņu proporciju izmaiņas augšanas laikā. **A**, starp starpspuru (is) un anālās peldspuras (as) dzelkšņiem; **B**, starp starpspuru (is) un krūšu peldspuras (ps) dzelkšņiem; **C**, starp iegurņa (pls) un krūšu peldspuras (ps) dzelkšņiem; **D**, starp iegurņa (pls) un anālās peldspuras (as) dzelkšņiem.

# Conclusions

The results of this study essentially contribute to the morphology, ontogeny, parasitology, palaeoecology and taphonomy of such early vertebrates as placoderms and acanthodians. Based on the detailed studies of excellently preserved juvenile fish collected by the author during the long-term excavations in the Lode clay quarry, Latvia, the sequence of ontogenetic stages of placoderm *Asterolepis ornata* and acanthodian *Lodeacanthus gaujicus* has been established using the newly developed research methodology of the early ontogeny. The observed morphological features of each developmental stage are reliable characters for distinguishing the developmental sequence of the dermal armour of placoderm and squamation of acanthodian, avoiding the description of the new taxa for each ontogeny stage or other misinterpretations in the future.

Taphonomical studies and careful morphofunctional analysis of all fossil remains from the Lode pit permitted to improve the existing hypotheses on the sedimentary environment within the transitional zone between the Devonian paleobasin and terrestrial environment and burial conditions of vertebrates, to establish several taphocoenoses within the Lode clay deposit, as well as allowed reconstruction of trophic relations, food chains and web within the palaeobiocenosis of the Lode time. The results obtained during this study demonstrate that the main aim of the promotion work has been reached and the main tasks accomplished. The results led to several important conclusions, which are grouped thematically into four chapters.

**A.** Taphonomical studies of fish remains, which allowed distinguish at least seven types of taphocoenoses differing in accordance with the dominant lithofacies of the fossil-bearing rocks, and re-evaluation of previously published data on the different orientation of fish skeletons of various taxa confirmed the hypothesis that fish carcasses were accumulated in the clayey sediments infilling the depressions on the slope of delta as a result of sorting of organism remains by weak currents. Hence, the hypothesis that the Lode oryctocoenosis of adult placoderms was formed in a result of a catastrophic mass mortality caused by anoxia in a shallowing basin (Lyarskaya, 1981, p.43) has not been proved. Taphonomical studies of juvenile fish remains confirmed the accumulation of them in lenses filled by the clayey mud. Presumably, that the Lode oryctocoenosis in "juvenile" fish lens would have been formed in a result of a catastrophic mass mortality caused by the slump processes on the submarine delta slope.

Reconstruction of trophic relations within the palaeobiocoenoses of the Lode time proposed here is suggested as typical for the deltaic zone of the Devonian palaeobasin. The food chains and web proposed here are based on studies of the abundant fossils of various organisms from different habitats and different trophic levels and consist of benthic and planktonic producers and consumers, organic detritus and plant remains, prey and predatory fishes. The statistical analysis of the exact number of fish individuals from different trophic levels testified the relation between the small amounts of predators to the large number of consumers. Parasitic organisms have been included in the trophic pyramid for the first time as well. The fossilized remains of stomach content of *Asterolepis* young, described for the first time, confirms the bottom dwelling life style for young individuals.

**B.** Morphological study of young individuals of antiarch placoderm fish from Lode and detailed comparison with adult individuals of *Asterolepis ornata* has confirmed that they belong to the same species despite the profound changes of the size and proportions of the whole body, shape and proportions of individual bones, structure and ornamentation of plates and scales, merging of several plates during the growth.

A number of morphological characters of immaturity have been defined allowing reconstruction of the sequence of development of the dermal armour. Five stages of early ontogeny have been established based on the set of quantitative and qualitative features specific for each ontogenetic stage, starting with the tiny fish represented by a weakly defined film of lightly ossified bony plates and squamation, with large ventral and lateral fenestrae in the trunk armour, and followed by the largest juvenile individuals, which already morphologically resemble the adult ones. The rate of the dermal armour growth was remarkably rapid, judging from the rate of appearance of new qualitative characters in a short range of the changing body size.

A full set of developmental stages demonstrates the remarkable allometric growth of *Asterolepis* during early ontogeny. The sequence of gradual changing of ornament includes smooth surface, irregular fine-meshed ornament, reticular, reticular ornament with radially arranged anastomosing ridges, radially arranged anastomosing ridges with tubercles, and tubercular ornament; more advanced stages of the ornament first appear on the dorsal side of the trunk armour and on the head. The three dimensional ornamentation increased the strength of the thin dermal armour plates. The determination of the each kind of the juvenile ornament provides possibility avoiding the misinterpretation of separately find fragments with different ornament as belonging to the new taxa in the future.

Well-developed ridge system of juvenile individuals is characteristic for early growth stages. Very thin dermal armour plates in early juvenile stages required a pronounced head and trunk ridge system as a framework for strength. The ridge system started to disappear when the thicker 3-layered bone is fully formed in advanced juveniles. Dermal armour initially developed along the ridges of the armour plate.

Remarkable differences in sutural connections between bony plates are indicated for juvenile and adult individuals: serratiform sutures are suggested to be one among the well marked characters of immaturity in *Asterolepis* and possibly in the related antiarch genera. The serratiform sutures appear firmer than the overlapped type, evidenced in the sequence of disintegration of fish bodies. In juveniles the sequence of disintegration slightly differs from that in adults due to growth peculiarities, gaps on the lateral and ventral walls.

Some ancestral features partly appear in the course of development of scales with a pit similarly to that in some Agnatha, as well as merging of the unnecessary sutures in subadult and adult individuals due to the presumably immobility of the corresponding plates (PDL+PL, $Cd_4$+ $Ml_5$+T).

**C.** The investigated acanthodian fish *Lodeacanthus gaujicus* presumably is the best-known Devonian acanthodian. *Lodeacanthus* represents a small genus of mesacanthid acanthodian and the largest individuals presumably are adults or at least nearly mature ones. The sequence of ontogenetic development is established and five stages of ontogenetic development are distinguished. Distinct scales with concave basements appear in *Lodeacanthus* in the early stages of ontogeny. Such scales are unknown in other acanthodians due to the absence of so small-size preserved juvenile individuals. Fully scaled individuals reveal the presence of six squamation zones of the body, allowing to avoiding the misinterpretation of separately find different scales as belonging to the new taxa in the future.

*Lodeacanthus* is closely related to *Triazeugacanthus* differing in having enlarged dermal bones in the cheek region and of a pair of nasal bones, longer and more numerous branchiostegal rays, the ornamentation of circumorbital bones and fin spines, and the morphology of the caudal fin. *Lodeacanthus* differs from both related genera *Triazeugacanthus* and *Mesacanthus* by the presence of dermal bones of the cheek region, a pair of nasal bones, and of scale covering on the base of the pectoral fins.

The morphology of acanthodian juveniles differs from adult individuals in several aspects. During the ontogenetic development the following changes are noticed: 1) in scale morphology and the extent of the scale covering; 2) in the shape of nasal bones; 3) in the increasing number of circumorbital bones; 4) in proportions of circumorbitals to prepectoral length; 5) in proportions of prepectoral length to total body length; 6) in proportions of fin spines; 7) in the gradual loss of the row of denticles on the anterior margins of the fin spines; 8) in the cross-section of the spines; 9) in the increasing relative height of the scapula; 10) in the shape of the hypochordal lobe.

*Lodeacanthus* exhibits a considerably faster rate of squamation development than other Acathodiformes. The squamation development is slightly different to that in juveniles of Carboniferous and Permian Acanthodidae (*Acanthodes*). The established sequence of ossification of skeletal elements in *Lodeacanthus* in overall is similar to that in *Acanthodes*. The first to ossify are the endoskeletal scapula and exoskeletal branchiostegal rays, then followed endocranium and exoskeletal head bones: circumorbital, nasal and cheek bones. Jaws and branchial arches become ossified only after the squamation extent is completely developed. The fin spines occurred more useable for the determination of the agedness than the total body length due to deformation changes of the scale covering during the process of fossilization.

**D.** Circlets of fossil hooks were found in young fish skeletons during the research of their morphology. The radially or parallel located hooks were identified as remains of parasitic organisms. Studies on the morphology of parasitic remains indicated that they might have been represented ancestors of different phyla Platyhelminthes and Acanthocephala, where hooks are used as attachment organ to the host. The discovery of parasitic remains in Devonian fish fossils confirmed the hypothesis of Llewellyn (1982) on phylogenesis of parasitic flatworms in fish. These remains could have represented ancestors of flatworms Monogenea. The maximum number of the hooks 16 evidenced that. It is characteristic to primitive monogeneans (Boeger, Kritsky, 1993).

The specific location of parasitic remains in juvenile fish bodies indicates they presumable belonging to representatives of ectoparasites and endoparasites. Small sized acanthodians possessed small sized hook systems of parasitic helminthes; larger acanthodians exhibit the greatest in size hook systems. Hence, parasites might have spent all their life in a one host.

Altogether remains of 77 parasitic worms were found in 16 juveniles of placoderm and in 27 acanthodian skeletons, as well as two in one individual of crustacean. Almost half of the found acanthodians exhibit invasion of parasites. The Late Devonian shallow sea in deltaic regions in Early Frasnian time was largely inhabited and the presence of a great number of infested fishes of at least two higher taxa of parasitic helminthes suggests of the high level of invasion.

The researched parasitic helminth remains in young fish bodies of placoderms and acanthodians are the oldest known fish parasites so far and represent the oldest host-parasitic associations ever found in the fossil record.

# APPENDICES

## 1. Abbreviations used in text and figures

### Index of anatomical abbreviations used for placoderms

**ac** - anterior corner of the Pi, Nu, SM, Sm, PMD, PDL, PVL plates,
**acr** - anterior cephalic ridge of the Prm, La plate,
**ad** – antero-dorsal corner of lateral lamina of the PVL plate,
**ad**$_1$ – anterior attachment area of the SM plate (prespiracular area),
**ad**$_2$ – posterior attachment area of the SM plate (postspiracular area),
**ADL** – anterior dorsolateral plate,
**al** – antero-lateral corner of subcephalic division of ventral lamina of the AVL plate,
**alc** - antero-lateral corner of trunk plates (Sm, AMD, PMD, PDL),
**alr** – anterior lateral ridge of the ADL plate,
**am** – antero-mesial corner of subcephalic division of ventral lamina of the AVL plate,
**amm** – anterior part of mesial margin of the La plate,
**AMD** – anterior median dorsal plate,
**an** – anterior notch of the Prm plate,
**aop** – anterior ornamented process of the R plate (of adult),
**ap** – anterior process of the R plate,
**AVL** – anterior ventrolateral plate,
**atvr** - anterior transverse ventral ridge of the AVL plate,
**Cd**$_1$ – dorsal central plate 1 of the pectoral fin,
**Cd**$_2$ – dorsal central plate 2 of the pectoral fin,
**Cd**$_3$ – dorsal central plate 3 of the pectoral fin,
**Cd**$_4$ – dorsal central plate 4 of the pectoral fin,
**cf.ADL** – area overlapping the ADL plate,
**cf.AMD** – area overlapping the AMD plate,
**cf.MxL** – area overlapping the MxL plate,
**cf.PDL** – area overlapping the PDL plate,
**cf.PMD** – area overlapping the PMD plate,
**cm**$_1$ – antero-medial corner of ventral lamina (before MV) of the PVL plate,
**cm**$_2$ – middle corner of ventral lamina (behind MV plate) of the PVL plate,
**cm**$_3$ – posterior medial corner of ventral lamina of the PVL plate,
**cr.pto** – postorbital crista of La, Pp plates,
**cr.tp** – crista transversalis interna posterior,
**Cv**$_1$ – ventral central plate 1,
**d** – dorsal corner of the PDL, PL, PVL plate,
**depr** – depression in the posterior part of the Nu plate,
**d.end**$_1$- dorsal openings of canal for ductus endolymphaticus on the Nu plate (of adult),
**dist** – distal segment of pectoral fin,
**dl** – dorso-lateral corner of the PDL plate,
**dlm** – dorsal lamina of trunk plates of the dorsal wall,
**dlp** – dorso-lateral process of the SO plate,
**dlr** – dorsolateral ridge of trunk armour (of the ADL and PDL plates),
**dm** – dorsal margin of the SM plate,
**dmr** – dorsal median ridge of trunk armour (of the AMD and PMD plates),
**dpp** - postpineal depression on the Nu plate,
**f** - groove on the AMD crossing contact face for the ADL plate,
**f.ax.** – foramen axillare of the AVL plate,
**f.art** - articular fossa of the ADL (of adult),

**fmp** – protractor area of processus brachialis of the AVL plate,
**ifc**$_1$ - part of infraorbital sensory line on the La, Prm, Pn plates (of adult),
**ifc**$_2$ - section of infraorbital sensory line on the SO plates (of adult),
**ispi** – infraspiracular notch of the SM plate,
**La** – lateral plate,
**lc** – lateral corner of the Nu, PMD, PDL plate,
**lcg** –main lateral line groove (of adult),
**llm** – lateral lamina of trunk plates of the lateral wall,
**m**$_1$ – anterior division of mesial margin of ventral lamina of the AVL in contact with the Sm plate,
**m**$_2$ – mesial division of mesial margin of ventral lamina of the AVL in contact with the second AVL plate,
**m**$_3$ – posterior division of mesial margin of ventral lamina of the AVL in contact with MV,
**ma**$_1$ – anterior division of medial margin of ventral lamina, connected with the MV plate,
**ma**$_2$ – posterior division of medial margin of ventral lamina, connected with corresponding division of medial lamina of the PVL of opposite side,
**mcr** - marginal cephalic ridge of the La, Pnu plate,
**Ml**$_2$ – lateral marginal plate 2 of pectoral fin,
**Ml**$_3$ – lateral marginal plate 3 of pectoral fin,
**Ml**$_4$ – lateral marginal plate 4 of pectoral fin,
**Ml**$_5$ – lateral marginal plate 5 of pectoral fin,
**Mm**$_2$ – mesial marginal plate 2 of pectoral fin,
**Mm**$_3$ – mesial marginal plate 3 of pectoral fin,
**Mm**$_4$ – mesial marginal plate 4 of pectoral fin,
**mpg** - middle pit-line groove on the Nu, Pn plates,
**mr** – median ridge on the Pp plate,
**MxL** – mixilateral plate (of adult),
**MV** – median ventral plate,
**na** – nasal opening of the R plate (of adult),
**nm** – obtected nuchal area (of subadult and adult),
**npn** - postnuchal notch of the AMD plate,
**Nu** – nuchal plate,
**oa.AMD** - area overlapped by the AMD plate,
**oa.AVL** - area overlapped by the AVL plate,
**oa.PMD** - area overlapped by the PMD plate,
**oa.PVL** – area overlapped by the PVL plate,
**orb** – orbital fenestra,
**otr** – oblique transverse ridge of the AMD and ADL plates,
**pc** – posterior corner of the Pi, Nu, La, ADL, PMD, PVL plate,
**pdc** – postero-dorsal corner of the PVL plate,
**PDL** – posterior dorsolateral plate,
**pfr** – ridge on the pectoral fin,
**Pi** – pineal plate,
**pi** – pineal opening on the Pi plate,
**PL** – posterior lateral plate,
**PL.ac** – anterior corner of the PL part of the MxL plate (of adult),
**plc** – postero-lateral corner of the AMD, PMD, ADL plate,
**pma** – posterior marginal area of the PMD plate,
**PMD** – posterior median dorsal plate,
**Pmg** – postmarginal plate,
**pmm** – posterior part of mesial margin of the La plate,

**pn** – posterior notch of the PMD plate,
**Pn** – paranuchal plate,
**Pp** – postpineal plate,
**ppr** - postpineal ridge of the Pp plate,
**pr** – paranasal process of the Prm plate,
**pr.br** – processus brachialis of the AVL plate,
**prc** – prepectoral corner of the AVL plate (of adult),
**pr.dm** – medial dorsal process of the PDL plate,
**Prm** – praemedial plate,
**pr.nm** – posterior median process of Nu plate (of subadult),
**pro** – processus obstans of the ADL plate,
**prox** – proximal segment of pectoral fin,
**pr.p** – posterior median process of the AMD plate,
**pr.pl** – external postlevator process the of AMD plate,
**pr.pn** – internal postlevator process of the ADL plate,
**pr.tv** – postero-ventral process of the PDL plate,
**ptc** – cephalic division of main lateral line of the Pn plate (of adult),
**ptdr -** posterior transverse dorsal ridge on the posterior part of the dorsal wall,
**ptlr** – posterior transverse lateral ridge,
**ptvr** - posterior transverse ventral ridge of the PVL plate,
**pvc** – postero-ventral corner of the PVL plate,
**PVL** – posterior ventrolateral plate,
**R** – rostrale,
**sad** - subanal division of the PVL plate,
**sar** – subanal ridges of the PVL plate,
**scr 1** – subcephalic ridge 1 of the AVL plate,
**scr 2** – subcephalic ridge 2 of the AVL plate,
**Sm** – semilunar plate,
**smr** - submarginal ridge of the SM plate,
**SM** – submarginal plate,
**sna** – supranuchal area of the AMD plate,
**sp** – spiracular groove of the La plate,
**SO** – suborbital plate,
**sol** – suborbital lamina of the La plate,
**sot** – supraotic thickening of the head-shield (of Nu plate),
**St** – fossilized stomach content,
**St.i.** – imprint of the fossilized stomach content (St located on the counterpart),
**T** – terminal plate of pectoral fin,
**tcr** - transverse cephalic ridge of the La, Nu plate,
**vlc** – ventro-lateral corner of the AVL plate,
**vlm** – ventral lamina of trunk plates of the ventral wall,
**vlp** – ventro-lateral process of the SO plate,
**vlr** – ventrolateral ridge of trunk armour (of AVL and PVL plates),
**vm** – ventral margin of the SM plate,
**vn** – ventral noch on the ventral margin of the PDL plate.

# Apzīmējumu saraksts bruņuzivīm

**ac** – Pi, Nu, SM, Sm, PMD, PDL, PVL plātņu priekšējais stūris,
**acr** –Prm, La kaulu priekšējais galvas valnītis,
**ad** –PVL plātnes sānu plaknes priekšējais dorsālais stūris,
**ad$_1$** –SM plātnes priekšējais stiprinājuma laukums,
**ad$_2$** –SM plātnes aizmugurējais stiprinājuma laukums,
**ADL** – priekšējā muguras-sānu plātne,
**al** – AVL plātnes vēdera plaknes zemgalvas reģiona priekšējais sānu stūris,
**alc** - rumpja plātņu (Sm, AMD, PMD, PDL plātnes) priekšējais sānu stūris,
**alr** – ADL plātnes priekšējais sānu valnītis,
**am** – AVL plātnes vēdera plaknes zemgalvas reģiona priekšējais mediālais stūris,
**amm** – La plātnes mediālās malas priekšējā daļa,
**AMD** – priekšējā vidējā muguras plātne,
**an** – Prm plātnes priekšējais ierobojums,
**aop** – R kaula priekšējais ornamentētais izaugums (pieaugušām bruņuzivīm),
**ap** – R kaula priekšējais izaugums,
**AVL** – priekšējā vēdera-sānu plātne,
**atvr** - AVL plātnes priekšējais šķērseniskais vēdera valnītis,
**Cd$_1$** – krūšu spuras pirmais centrālais dorsālais kauls,
**Cd$_2$** – krūšu spuras otrais centrālais dorsālais kauls,
**Cd$_3$** – krūšu spuras trešais centrālais dorsālais kauls,
**Cd$_4$** – krūšu spuras ceturtais centrālais dorsālais kauls,
**cf.ADL** – pārsedzes laukums ADL plātnei,
**cf.AMD** – pārsedzes laukums AMD plātnei,
**cf.MxL** – pārsedzes laukums MxL plātnei,
**cf.PDL** – pārsedzes laukums PDL plātnei,
**cf.PMD** – pārsedzes laukums PMD plātnei,
**cm$_1$** – PVL plātnes vēdera sieniņas priekšējais-mediālais stūris (pirms MV kaula),
**cm$_2$** – PVL plātnes vēdera sieniņas vidējais stūris (aiz MV kaula),
**cm$_3$** – PVL plātnes vēdera sieniņas aizmugurējais stūris,
**cr.pto** – La, Pp plātņu aizorbitālais valnītis,
**cr.tp** – aizmugurējais iekšējais šķērseniskais valnītis,
**Cv$_1$** – krūšu spuras pirmais centrālais vēdera kauls,
**d** – PDL, PL, PVL plātņu dorsālais stūris,
**depr** – padziļinājums Nu plātnes aizmugurējā daļā,
**d.end$_1$**- endolimfatisko vadu mugurējās atveres Nu plātnes virsmā (pieaugušiem īpatņiem),
**dist** – krūšu spuras distālais segments,
**dl** – PDL plātnes muguras-sānu stūris,
**dlm** – rumpja plātņu muguras sieniņas,
**dlp** – SO kaula dorsālais-sānu izvirzījums,
**dlr** – ADL un PDL plātņu muguras-sānu valnītis,
**dm** – SM plātnes dorsālā mala,
**dmr** – AMD un PMD plātņu dorsāli-mediālais valnītis,
**dpp** - Nu plātnes aizpineālais ierobojums,
**f** - AMD un ADL plātņu kontaktvirsmas rieva,
**f.ax.** – AVL plātnes paduses atvere
**f.art** - ADL plātnes locītavas bedre (pieaugušiem īpatņiem)
**fmp** – AVL plātnes rokas izauguma *protractor* laukums,
**ifc$_1$** - infraorbitālās sānu līnijas daļa uz La, Prm, Pn plātnēm (pieaugušiem īpatņiem),
**ifc$_2$** - infraorbitālās sānu līnijas daļa uz SO plātnes (pieaugušiem īpatņiem),

**ispi** – SM plātnes infraspirakulārais ierobojums,
**La** – sānu plātne,
**lc** –Nu, PMD, PDL plātņu sānu stūris,
**lcg** – galvenās sānu līnijas rieva (pieaugušām bruņuzivīm),
**llm** – rumpja kaulu sānu sienas laterālā plātne,
**m**$_1$ – AVL plātnes vēdera plaknes vidus malas priekšējā daļa, gar kuru AVL kontaktē ar Sm plātni,
**m**$_2$ – AVL plātnes vēdera plaknes vidus malas vidējā daļa, gar kuru AVL kontaktē ar pretējo AVL plātni,
**m**$_3$ – AVL plātnes vēdera plaknes vidus malas pakaļējā daļa, gar kuru AVL kontaktē ar MV plātni,
**ma**$_1$ **-** ventrālās plaknes priekšējā nodalījuma mediālā mala, kas kontaktē ar MV plātni,
**ma**$_2$ – ventrālās plaknes aizmugurējā nodalījuma mediālā mala, kas kontaktē ar atbilstošu nodalījumu PVL plātnes mediālajai plaknei,
**mcr** - La, Pnu plātņu malējais galvas valnītis,
**Ml**$_2$ – krūšu spuras otrais sānu malas kauls,
**Ml**$_3$ – krūšu spuras trešais sānu malas kauls,
**Ml**$_4$ – krūšu spuras ceturtais sānu malas kauls,
**Ml**$_5$ – krūšu spuras piektais sānu malas kauls,
**Mm**$_2$ – krūšu spuras otrais sānu vidējais kauls,
**Mm**$_3$ – krūšu spuras trešais sānu vidējais kauls,
**Mm**$_4$ – krūšu spuras ceturtais sānu vidējais kauls,
**mpg** - vidējā *pit-line* rieva uz Nu, Pn plātnēm,
**mr** – mediālais valnītis uz Pp plātnes,
**MxL** – pakaļējā muguras-sānu plātne (pieaugušām bruņuzivīm),
**MV** – vidējā ventrālā plātne,
**na** – R plātnes nāsu atvērumu vieta (pieaugušām bruņuzivīm),
**nm** – *obtected nuchal area* (pusaugu un pieaugušām bruņuzivīm),
**npn** - aizpakauša ierobojums uz AMD plātnes,
**Nu** – pakauša kauls/plātne,
**oa.AMD** - ar AMD plātni segtais pārsedzes laukums,
**oa.AVL** - ar AVL plātni segtais pārsedzes laukums,
**oa.PMD** - ar PMD plātni segtais pārsedzes laukums,
**oa.PVL** – ar PVL plātni segtais pārsedzes laukums,
**orb** – acu dobums,
**otr** – slīpais šķērseniskais valnītis uz AMD un ADL plātnēm,
**pc** – aizmugurējais stūris uz Pi, Nu, La, ADL, PMD, PVL plātnēm,
**pdc** –PVL plātnes pakaļējais muguras stūris,
**PDL** – pakaļējā muguras-sānu plātne,
**pfr** – krūšu spuras valnītis,
**Pi** – pineālais kauls,
**pi** – pineālais atvērums uz Pi kaula,
**PL** – pakaļējā-sānu plātne,
**PL.ac** – MxL plātnes pakaļējās sānu daļas priekšējais stūris (pieaugušām bruņuzivīm),
**plc** – pakaļējais-sānu stūris uz AMD, PMD, ADL plātnēm,
**pma** –PMD plātnes pakaļējā sānu mala,
**PMD** – pakaļējā muguras plātne,
**Pmg** – pakaļējās malas plātne,
**pmm** – La (sānu) plātnes pakaļējās daļas mediālā mala,
**pn** – PMD plātnes aizmugurējais ierobojums,
**Pn** – sānu pakauša kauls,

**Pp** – pakaļējais pinealais kauls,
**ppr** –Pp kaula aizpineālais valnītis,
**pr** – Prm plātnes blakusdeguna izaugums,
**pr.br** – AVL plātnes rokas izaugums,
**prc** –AVL plātnes pirmskrūšspuras stūris,
**pr.dm** – PDL plātnes mediālais muguras izvirzījums,
**Prm** – priekšējais nepāra kauls,
**pr.nm** –Nu (pakauša) kaula pakaļējais mediālais izvirzījums (pusaugu indivīdiem),
**pro** – ADL plātnes izturīgs izaugums,
**prox** – krūšu spuras proksimālais segments,
**pr.p** –AMD kaula pakaļējais mediālais izvirzījums,
**pr.pl** – ADL plātnes ārējais postlevatora izaugums,
**pr.pn** – ADL plātnes iekšējais postlevatora izaugums,
**pr.tv** – PDL plātnes pakaļējais ventrālais izvirzījums,
**ptc** – galvenās sānu līnijas galvas daļa uz Pn plātnes,
**ptdr -** šķērseniskais pakaļējais muguras valnītis,
**ptlr** – šķērseniskais pakaļējais sānu valnītis,
**ptvr** - PVL plātnes pakaļējais šķērseniskais vēdera valnītis,
**pvc** – PVL plātnes pakaļējais-vēdera stūris,
**PVL** – pakaļējais vēdera-sānu kauls,
**R** – rostrālais kauls,
**sad** - PVL kaula pieanālā (subanālā) daļa/nodalījums,
**sar** – subanālie valnīši uz PVL kaula,
**scr 1** – pirmais zemgalvas valnītis uz AVL plātnes,
**scr 2** – otrais zemgalvas valnītis uz AVL plātnes,
**Sm** – pusmēness kauls,
**smr** - submarginālais valnītis uz žaunu vāka,
**SM** – žaunu vāks,
**sna** –AMD plātnes virspakauša laukums,
**sp** – spirakulārā rieva uz La (sānu) kaula,
**SO** – zemacu kauls,
**sol** – La kaula pieacu dobuma plātne,
**sot** –galvaskausa vairoga virsacu sabiezinājums,
**St** – fosilizēts kuņģa saturs,
**St.i.** – fosilizēta kuņģa satura iespiedums,
**T** – krūšu spuras galējais kauls,
**tcr** - šķērseniskais galvas valnītis uz La, Nu kauliem,
**vlc** – AVL plātnes vēdera-sānu stūris,
**vlm** – vēdera sieniņas rumpja kaulu vēdera plātnes,
**vlp** –SO (zemacu) kaula vēdera-sānu izvirzījums,
**vlr** – vēdera-sānu valnītis uz rumpja kauliem (AVL un PVL kauliem),
**vm** –SM kaula vēdera mala,
**vn** – PDL plātnes vēdera malas ventrālais ierobojums.

| **Index of anatomical abbreviations used for acanthodians** | **Apzīmējumu saraksts akantodēm** |
|---|---|
| **art.c** - articular cotylus, | **art.c** - locītavas bedrīte |
| **art.pr** - articular process, | **art.pr** – vai locītavas izaugums, |
| **as** - anal fin spine, | **as** – anālās spuras dzelksnis, |
| **axl** - axial lobe, | **axl** – aksiālā daiva, |
| **br.a** - branchial arches, | **br.a –** žaunu loki, |
| **b.pr** - basal process, | **b.pr** – bazālais izvirzījums (izaugums?), |
| **br.r** - branchiostegal rays, | **br.r** – branhiostegālie stari, |
| **cb** - cheek bones, | **cb** – vaigu kauli, |
| **co** - circumorbital bones, | **co** – cirkumorbitālie kauli, |
| **ds** - dorsal fin spine, | **ds** – muguras spuras dzelksnis, |
| **en** – fragments of endocranium brūnie (redish patches), | **en** – smadzeņu kapsulas fragments (sarkanīgi plankumi) |
| **epl** - epichordal lobe, | **epl** – epihordālā daiva, |
| **es** – eye stain, | **es** – acs krāsviela, |
| **ex pq** – extrapalatoquadrate ridge, | **ex pq** – ārējais aukslēju-kvadrāta valnītis |
| **fr** - fragment of second nasal bone, | **fr** – fragments no otrā deguna kaula, |
| **hcl** - hypochordal lobe, | **hcl** – hipohordālā daiva, |
| **infr** - infraorbital sensory line, | **infr** – starpacu jūtīgā (sensorā) līnija, |
| **im** - imprints of scale bases, | **im** – zvīņu pamatņu nospiedumi, |
| **is** - intermediate fin spine, | **is** – starpspuru dzelksnis, |
| **mk** - Meckelian element, | **mk** – Mekeļa skrimlis, |
| **mll** – main lateral line, | **mll** – galvenā sānu līnija, |
| **na** - nasal bones, | **na** – deguna kauli, |
| **ot. c** - otic cotylus, | **ot. c** - auss bedrīte |
| **pls** - pelvic fin spine, | **pls** – iegurņa spuras dzelksnis, |
| **preart. pr** - prearticular process, | **preart. pr** – pirmslocītavas izaugums, |
| **ps** - pectoral fin spine, | **ps** – krūšu spuras dzelksnis, |
| **pq** - palatoquadrate, | **pq** – aukslēju-kvadrāta kauls, |
| **sc** – scapula. | **sc** – lāpstiņas kauls. |

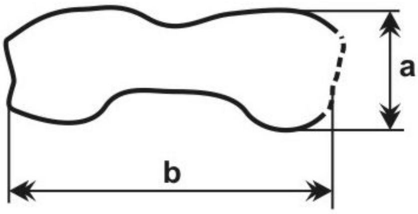
## 2. Measurements and indicated distances of the head-shield and trunk armour plates of juveniles and adults of placoderm *Asterolepis ornata*

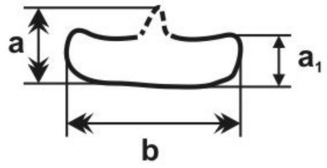
### 2.1. Premedian plate (Prm)

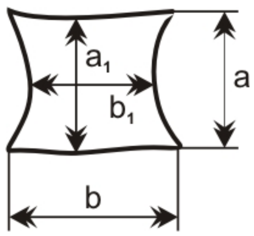
| Length (a), width (b), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | Adult | Adult* |
| | 1 | 2 | 3 | | |
| **a** | (0.30) n=1 | 0.55-1.00 n=8 | 1.30-1.40 n=2 | 18.0-35.5 n=4 | 30.0-34.0 n=2 |
| **b** | (1.55) n=1 | 2.40-2.80 n=7 | ~3.80 n=1 | 30.3-42.2 n=8 | 43.0-50.0 n=2 |
| **a / b** | 0.19 n=1 | 0.20-0.36 n=7 | 0.37 n=1 | 0.43-0.83 n=4 | 0.68-0.70 n=2 |

n – number of measured specimens;
Adult* - measurements from Karatajūte-Talimaa (1963, p. 156 – after Gross, 1931, Stensio, 1931).
Measurements in brackets indicate that the values have been estimated taking into account the distance between the neighboring lateral plates.

**2.1. Premedian plate** (juvenile) **2.2. Rostrale** (juvenile) **2.3. Pineale**
(juvenile)







### 2.2. Rostral plate (R)

| Length (a-$a_1$), width (b), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | 0.45 n=1 | 0.50-0.65 n=8 | - | - | 6.0-7.1 n=3 |
| **$a_1$** | 0.35 n=1 | 0.40-0.55 n=9 | - | 0.80 n=1 | 3.2-4.5 n=5 |
| **b** | 1.00 n=1 | 1.35-1.60 n=10 | - | 2.25 n=1 | 15.9-27.0 n=4 |
| **a / b** | 0.45 n=1 | 0.34-0.43 n=8 | - | - | 0.27-0.38 n=3 |
| **$a_1$ / b** | 0.35 n=1 | 0.30-0.34 n=8 | - | 0.36 n=1 | 0.12-0.24 n=4 |

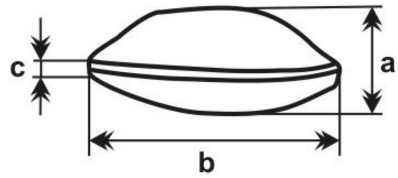
### 2.3. Pineal plate (Pi)

| Length (a-$a_1$), width (b-$b_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juvenile individuals, stage of ontogeny | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 0.95-1.25 n=8 | 1.40-2.00 n=2 | - | 11.5-13.0 n=4 |
| **$a_1$** | 0.50 n=1 | 0.80-1.10 n=9 | 1.20-1.50 n=3 | - | 9.2-15.0 n=5 |
| **b** | - | 1.20-1.60 n=9 | 1.80-2.50 n=2 | 2.70 n=1 | 25.5-29.3 n=4 |
| **$b_1$** | 0.50 n=1 | 0.88-1.10 n=12 | 1.20-1.50 n=3 | 1.85 n=1 | 10.5-15.8 n=5 |
| **a / b** | - | 0.63-0.79 n=6 | 0.78-0.80 n=2 | - | 0.41-0.50 n=4 |
| **$a_1$ / $b_1$** | 1.00 n=1 | 0.81-1.00 n=8 | 1.00 n=3 | - | 0.67-0.80 n=4 |

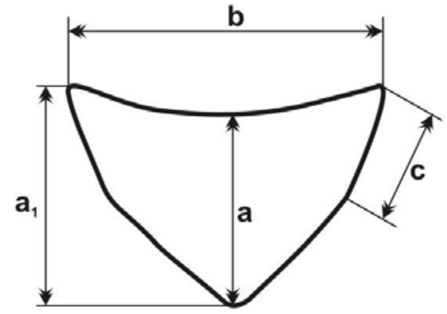
### 2.4. Postpineal plate (Pp)

| Length (a, c), width (b), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Juveniles | | | | | Sub-adult | Adult |
| | 1 | 2 | 3 | 4 | 5 | | |
| **a** | 0.55 n=1 | 0.50-0.95 n=16 | 1.10-1.30 n=5 | 1.90 n=1 | 2.50 n=1 | 11.2 n=1 | 15.0-20.5 n=19 |
| **b** | 1.40 n=1 | 1.40-2.00 n=12 | 2.25-2.65 n=4 | 3.80 n=1 | 5.00 n=1 | 19.4 n=1 | 24.4-32.5 n=19 |
| **c** | - | 0.10 n=1 | 0.40-0.60 n=4 | 0.65 n=1 | 0.80 n=1 | - | 7.7-12.5 n=16 |
| **a / b** | 0.39 n=1 | 0.41-0.45 n=12 | 0.46-0.49 n=4 | 0.50 n=1 | 0.50 n=1 | 0.59 n=1 | 0.53-0.64 n=19 |
| **a/c** | - | 8.00 n=1 | 2.00-2.88 n=4 | 2.92 n=1 | 3.13 n=1 | - | 1.46-2.03 n=16 |

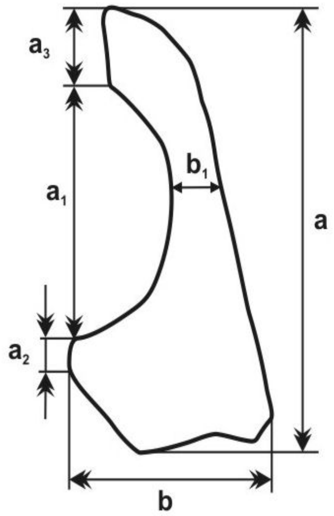
**2.4. Postpineale** (juvenile)
(juvenile)



**Postpineale** (adult)



**2.5. Laterale**



### 2.5. Lateral plate (La)

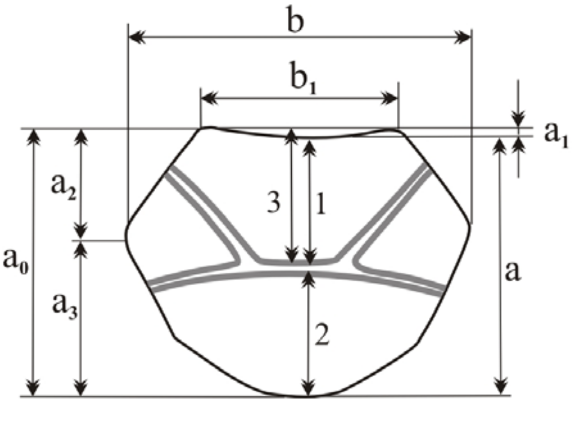
| Length ($a$-$a_3$), width ($b$-$b_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Juveniles | | | | Sub-adult | Adult | Adult* |
| | 1 | 2 | 3 | 4 | | | |
| **a** | 2.90 n=1 | 3.20-4.30 n=19 | 4.45-6.00 n=5 | 6.20 n=1 | 17.6 n=1 | 34.4-51.0 n=19 | 51.0-58.0 n=4 |
| **$a_1$** | 1.70 n=1 | 1.90-2.30 n=22 | 2.40-2.70 n=5 | 2.80 n=1 | ~6.8 n=1 | 13.4-17.6 n=18 | - |
| **$a_2$** | 0.25 n=1 | 0.30-0.35 n=13 | 0.45-0.80 n=6 | 0.90 n=1 | 3.5 n=1 | 7.5-12.9 n=17 | 10.0-12.0 n=4 |
| **$a_3$** | 0.40 n=1 | 0.60-0.90 n=19 | 1.00-1.15 n=5 | - | ~6.1 n=1 | 12.5-19.1 n=18 | 20.0 n=4 |
| **b** | 1.70 n=1 | 2.00-2.40 n=20 | 2.40-3.30 n=8 | 3.30 n=1 | 8.8 n=1 | 22.4-38.2 n=19 | 34.0-37.0 n=4 |
| **$b_1$** | ? 0.50 n=1 | 0.50-0.80 n=21 | 0.90-1.10 n=4 | - | 3.9 n=1 | 9.7-17.6 n=19 | 14.7-15.5 n=4 |
| **$a / a_1$** | 1.71 n=1 | 1.76-1.90 n=19 | 1.85-1.95 n=7 | 2.21 n=1 | 2.59 n=1 | 2.71-3.19 n=14 | - |
| **$a / a_2$** | 11.60 n=1 | 10.67-13.0 n=11 | 9.56-7.50 n=6 | 6.89 n=1 | 5.03 n=1 | 4.08-4.96 n=15 | - |
| **$a / a_3$** | 7.25 n=1 | 5.69-4.12 n=19 | 5.56-4.50 n=5 | - | 2.88 n=1 | 3.34-2.18 n=18 | - |
| **a / b** | 1.71 n=1 | 1.72-1.83 n=17 | 1.82-1.93 n=5 | 1.88 n=1 | 2.0 n=1 | 1.33-1.67 n=20 | 1.57-1.94 n=4 |
| **$a / b_1$** | ? 5.80 n=1 | 4.30-5.71 n=13 | 5.33-5.56 n=3 | - | 4.51 n=1 | 3.28-3.72 n=16 | 3.40-3.74 n=4 |

Adult* - measurements from Karatajūte-Talimaa (1963, p. 158 – after Gross, 1931, Stensio, 1931).

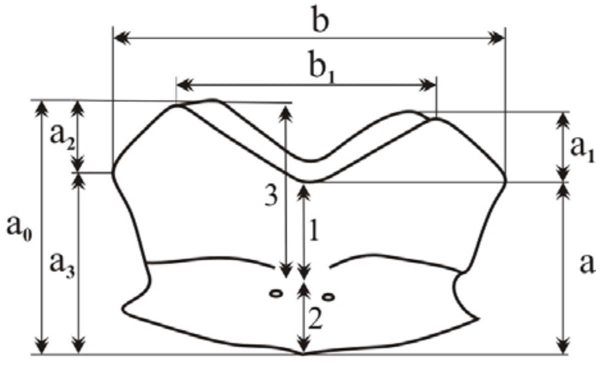
## 2.6. Nuchal plate (Nu)

| Length ($a_0$-$a_3$,1-3) width (b-$b_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Juveniles | | | | | Subadult | Adult |
| | 1 | 2 | 3 | 4 | 5 | | |
| **a** | 2.00 n=1 | 2.15-2.35 n=18 | 2.40-2.80 n=7 | 2.95 n=1 | 3.80 n=1 | 9.00-14.30 n=7 | 17.00-24.0 n=15 |
| **$a_0$** | 2.10 n=1 | 2.15-2.60 n=18 | 2.65-3.30 n=7 | 3.50 n=1 | 4.50 n=1 | 10.50-18.6 n=6 | 22.00-39.2 n=11 |
| **$a_1$** | 0.10 n=1 | 0.10-0.25 n=20 | 0.25-0.50 n=7 | 0.55 n=1 | 0.70 n=1 | 1.90-5.00 n=6 | 6.00-10.40 n=13 |
| **$a_2$** | 0.45 n=1 | 0.60-1.00 n=17 | 1.00-1.20 n=4 | 1.20 n=1 | 1.90 n=1 | 1.80-5.00 n=6 | 6.90-13.10 n=10 |
| **$a_3$** | 1.65 n=1 | 1.50-1.60 n=12 | 1.65-2.10 n=6 | 2.30 n=1 | 2.60 n=1 | 8.70-13.60 n=6 | 15.10-26.10 n=11 |
| **b** | 2.60 n=1 | 3.00-3.80 n=21 | 4.00-5.20 n=6 | 5.65 n=1 | 7.00 n=1 | 17.80-32.0 n=7 | 39.00-53.50 n=18 |
| **$b_1$** | - | 1.60-1.85 n=10 | 2.00-2.50 n=7 | 3.20 n=1 | 4.20 n=1 | 9.60-16.20 n=7 | 22.60-32.00 n=18 |
| **$a_0$/ b** | 0.81 n=1 | 0.66-0.77 n=20 | 0.63-0.70 n=6 | 0.62 n=1 | 0.64 n=1 | 0.48-0.64 n=6 | 0.55-0.67 n=10 |
| **$a_0$ / $a_1$** | 21.0 n=1 | 12.75-23.0 n=18 | 6.60-10.40 n=8 | 6.36 n=1 | 6.43 n=1 | 5.53-3.52 n=6 | 3.72-3.21 n=9 |
| **$a_2$ / $a_3$** | 0.27 n=1 | 0.29-0.60 n=14 | 0.40-0.67 n=7 | 0.52 n=1 | 0.73 n=1 | 0.21-0.47 n=6 | 0.31-0.47 n=10 |
| **1** | 1.10 n=1 | 1.20-1.50 n=18 | 1.60-2.00 n=5 | 2.15 n=1 | 2.70 n=1 | 6.50 n=1 | 14.00 n=1 |
| **2** | 1.00 n=1 | 0.90-1.10 n=19 | 1.10-1.30 n=4 | 1.35 n=1 | 1.80 n=1 | 4.50 n=1 | 10.00 n=1 |
| **3** | 1.20 n=1 | 1.35-1.70 n=15 | 1.85-2.50 n=5 | 2.70 n=1 | 3.40 n=1 | 10.30 n=1 | 24.40 n=1 |
| **1/2** | 1.10 n=1 | 1.20-1.50 n=16 | 1.50-1.60 n=5 | 1.59 n=1 | 1.50 n=1 | 1.44 n=1 | 1.40 n=1 |
| **3/2** | 1.20 n=1 | 1.40-1.70 n=13 | 1.77-1.92 n=5 | 2.00 n=1 | 1.88 n=1 | 2.29 n=1 | 2.44 n=1 |
| **b / $b_1$** | - | 1.73-2.20 n=11 | 1.82-2.08 n=5 | 1.77 n=1 | 1.67 n=1 | 1.65-1.98 n=5 | 1.53-1.89 n=21 |

**2.6. Nuchale** (juvenile)



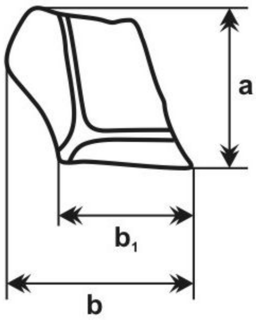
**Nuchale** (adult)

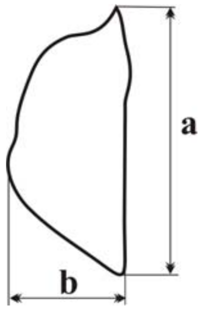


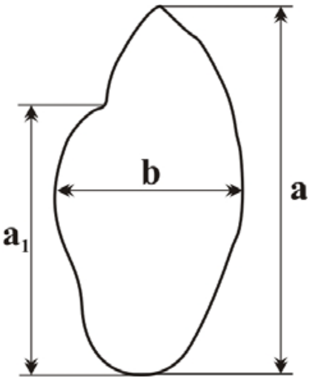
### 2.7. Paranuchal plate (Pn)

| Length (a), width (b-b$_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 1.50-1.60 n=3 | 2.00 n=1 | 2.10 n=1 | 16.5-25.3 n=8 |
| **b** | - | 1.70-2.20 n=4 | 2.25 n=1 | 2.70 n=1 | 21.7-26.0 n=7 |
| **b$_1$** | - | 0.90-1.25 n=2 | 1.80 n=1 | 2.00 n=1 | - |
| **a / b** | - | 0.88-0.94 n=3 | 0.89 n=1 | 0.78 n=1 | 0.76-0.94 n=7 |
| **a / b$_1$** | - | 1.67-1.28 n=2 | 1.11 n=1 | 1.05 n=1 | - |

**2.7. Paranuchale** (juvenile) **2.8. Postmarginale** (juvenile) **2.9. Submarginale** (juvenile)







### 2.8. Postmarginal plate (Pmg)

| Length (a), width (b), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | |
|---|---|---|---|---|---|---|
| | Juveniles | | | | | Adult |
| | 1 | 2 | 3 | 4 | 5 | |
| **a** | - | - | 2.20 n=1 | - | 3.00 n=1 | 23.1-34.0 n=11 |
| **b** | - | - | 0.90 n=1 | - | 1.50 n=1 | 11.2-16.8 n=9 |
| **a / b** | - | - | 2.44 n=1 | - | 2.00 n=1 | 1.90-2.48 n=10 |

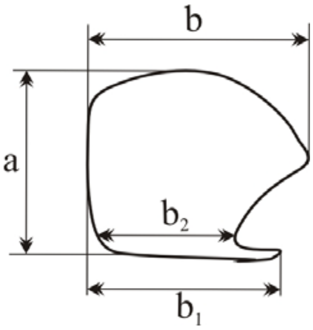
### 2.9. Submarginal plate (SM)

| Length (a-a$_1$), width (b), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 2.40-4.35 n=20 | 4.50 n=1 | - | - |
| **a$_1$** | - | 2.30-3.15 n=17 | 3.20 n=1 | - | - |
| **b** | - | 1.60-2.15 n=20 | 2.25-2.30 n=2 | - | - |
| **a / b** | - | 1.89-2.21 n=16 | 1.96 n=1 | - | - |
| **a$_1$ / b** | - | 1.28-1.59 n=18 | 1.39 n=1 | - | - |

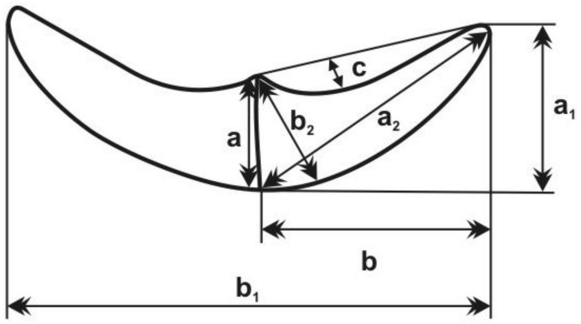
## 2.10. Suborbital plate (SO)

| Length (a), width (b-$b_2$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 1.25-1.60 n=7 | 1.90 n=1 | - | 25.5 n=1 |
| **b** | - | 1.65-2.05 n=8 | 2.30 n=1 | - | 31.0 n=1 |
| **$b_1$** | - | 1.20-2.15 n=6 | 2.15 n=1 | - | 27.5 n=1 |
| **$b_2$** | - | 0.60-1.45 n=8 | 1.50 n=1 | - | 19.0 n=1 |
| **a / b** | - | 0.67-0.76 n=5 | 0.70 n=1 | - | 0.82 n=1 |

**2.10. Suborbitale** (juvenile)



**2.11. Semilunare** (juvenile)



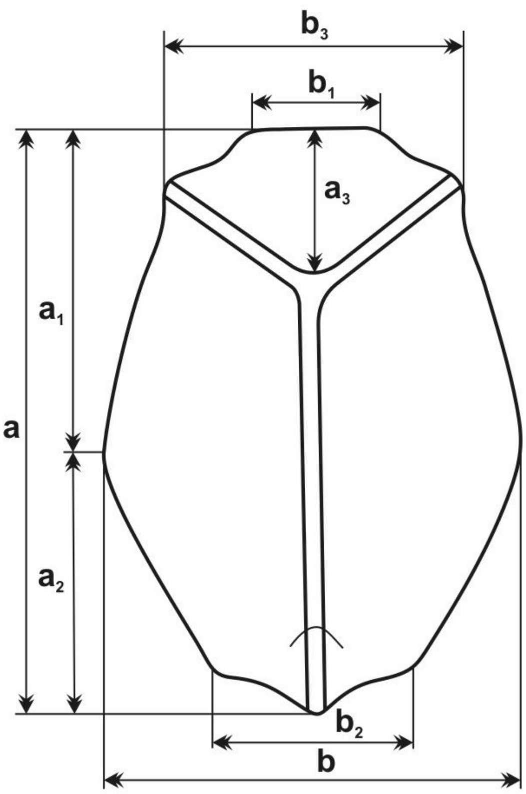
## 2.11. Semilunar plate (Sm)

| Length (a-$a_2$), width (b-$b_2$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 0.80-1.20 n=8 | - | - | 16.0 n=1 |
| **$a_1$** | - | 1.30-2.00 n=7 | - | - | 11.4-22.0 n=2 |
| **$a_2$** | - | 2.25-2.90 n=7 | - | - | 27.1-35.0 n=2 |
| **b** | - | 1.65-2.00 n=8 | - | - | 25.1-31.0 n=2 |
| **$b_1$** | - | 3.40-4.15 n=7 | - | - | 50.0-62.0 n=2 |
| **$b_2$** | - | 0.90-1.00 n=7 | - | - | 12.0-19.0 n=2 |
| **c** | - | 0.30-0.45 n=7 | - | - | 2.5-3.0 n=2 |
| **a / b** | - | 0.47-0.61 n=8 | - | - | 0.52 n=1 |
| **a / $a_1$** | - | 0.59-0.68 n=8 | - | - | 0.73 n=1 |
| **$a_2$ / $b_2$** | - | 2.40-3.22 n=7 | - | - | 1.84-2.26 n=2 |
| **c / $a_2$** | - | 0.13-0.21 n=7 | - | - | 0.07-0.11 n=2 |

## 2.12. Anterior median dorsal plate (AMD)

| Length (a-$a_3$), width (b-$b_3$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Juveniles | | | | | Subadult | Adult |
| | 1 | 2 | 3 | 4 | 5 | | |
| **a** | 4.50-4.60 n=2 | 4.80-7.30 n=34 | 7.50-9.00 n=6 | - | 13.8 n=1 | 24.0-69.5 n=4 | 106.0-182.0 n=30 |
| $\mathbf{a_1}$ | - | 2.70-3.80 n=32 | 4.00-4.80 n=5 | - | 7.20 n=1 | 13.5-38.2 n=4 | 54.0-104.5 n=25 |
| $\mathbf{a_2}$ | - | 2.20-3.50 n=26 | 3.40-4.35 n=3 | - | - | 10.5-31.3 n=4 | 52.0-85.0 n=22 |
| $\mathbf{a_3}$ | 1.30-1.50 n=2 | 1.40-2.10 n=34 | 2.30-3.70 n=5 | 4.60 n=1 | 5.20 n=1 | - | - |
| **b** | 3.00-3.40 n=2 | 4.00-5.20 n=37 | 5.40-6.60 n=10 | 8.40 n=1 | 8.80 n=1 | 15.0-46.0 n=4 | 72.0-122.0 n=31 |
| $\mathbf{b_1}$ | 1.40 n=1 | 1.40-1.60 n=31 | 1.80-2.00 n=6 | 2.00 n=1 | 2.00 n=1 | 3.5-6.5 n=4 | 10.5-25.4 n=23 |
| $\mathbf{b_2}$ | - | 1.80-2.60 n=20 | 3.00-3.20 n=3 | - | - | 9.0-25.0 n=3 | 34.0-64.0 n=29 |
| $\mathbf{b_3}$ | 1.70-2.40 n=2 | 2.60-3.40 n=38 | 4.00-4.50 n=4 | 6.20 n=1 | 6.40 n=1 | 24.4 n=1 | 37.0-89.0 n=14 |
| **a / b** | 1.35-1.50 n=2 | 1.18-1.39 n=35 | 1.36-1.46 n=4 | - | 1.57 n=1 | 1.51-1.63 n=4 | 1.34-1.68 n=34 |
| $\mathbf{a / a_1}$ | - | 1.73-1.92 n=29 | 1.81-1.99 n=3 | - | 1.92 n=1 | 1.78-1.89 n=4 | 1.76-2.08 n=28 |
| $\mathbf{b / b_1}$ | 2.43 n=1 | 2.63-3.38 n=34 | 3.00-3.67 n=5 | - | 4.40 n=1 | 4.29-8.22 n=4 | 4.51-9.65 n=22 |
| $\mathbf{b / b_3}$ | 1.42 n=1 | 1.40-1.65 n=37 | 1.35-1.65 n=5 | - | 1.38 n=1 | 1.89 n=1 | 1.54-2.05 n=14 |
| $\mathbf{b_1 / b_2}$ | - | 0.68-0.95 n=18 | 0.56-0.67 n=2 | - | - | 0.18-0.40 n=3 | 0.22-0.46 n=22 |

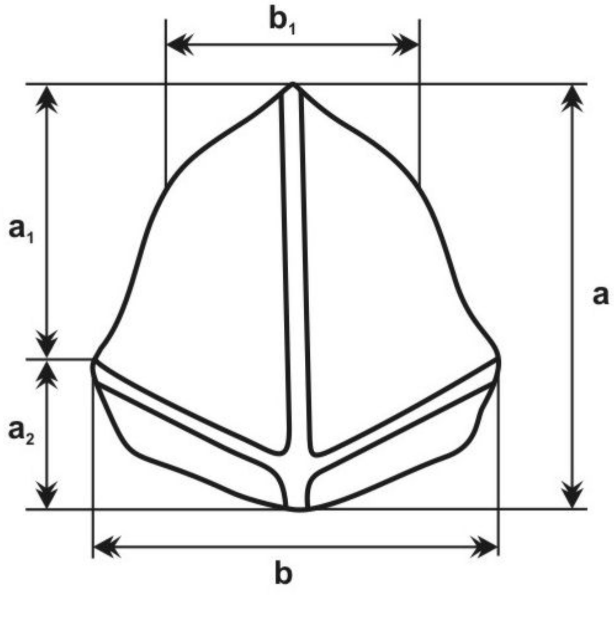
**2.12. AMD** (juvenile)



## 2.13. Posterior median dorsal plate (PMD)

| Length (a-a$_2$), width (b-b$_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Juveniles | | | | | Subadult | Adult n – 13-18 |
| | 1 | 2 | 3 | 4 | 5 | | |
| **a** | - | 2.40-3.40 n=8 | 3.60-3.80 n=2 | 5.60 n=1 | - | 20.1-40.5 n=4 | 74.9-127.0 n=18 |
| **a$_1$** | - | 1.50-2.30 n=9 | 2.10-2.30 n=2 | 3.30 n=1 | - | 17.6-27.9 n=3 | 53.0-89.0 n=15 |
| **a$_2$** | - | 1.10-1.25 n=8 | 1.50 n=2 | 2.30 n=1 | - | 12.6 n=1 | 20.4-32.0 n=12 |
| **b** | - | 2.00-3.30 n=13 | 3.40-3.60 n=2 | 5.60 n=1 | - | 29.2-44.0 n=4 | 79.0-133.0 n=18 |
| **b$_1$** | - | 2.00-2.40 n=11 | 2.20-2.70 n=2 | 3.30 n=1 | - | 16.0-26.0 n=2 | 42.0-58.4 n=14 |
| **a / b** | - | 1.03-1.20 n=7 | 1.00-1.12 n=2 | 1.00 n=1 | - | 0.69-1.10 n=4 | 0.80-1.21 n=18 |
| **a$_1$ / a$_2$** | - | 1.25-1.91 n=5 | 1.40-1.53 n=2 | 1.43 n=1 | - | 2.21 n=1 | 2.42-3.62 n=12 |
| **a / a$_1$** | - | 1.52-1.80 n=6 | 1.65-1.71 n=2 | 1.70 n=1 | - | 1.07-1.45 n=3 | 1.28-1.44 n=14 |

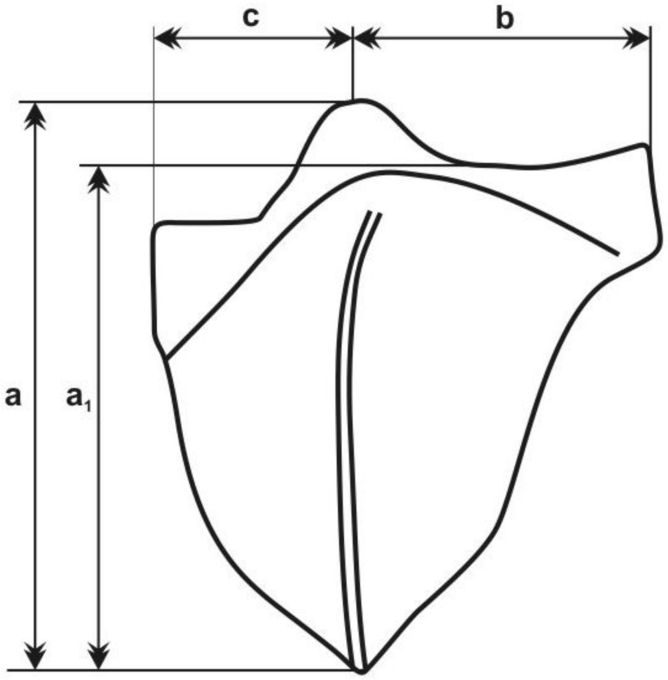
**2.13. PMD** (juvenile)



## 2.14. Anterior dorso lateral plate (ADL)

| Length ($a$-$a_1$), width(b), high (c), mm | Stages of ontogeny of *Asterolepis ornata* | | | | | |
|---|---|---|---|---|---|---|
| | Juveniles | | | | Subadult | Adult |
| | 1 | 2 | 3 | 4 | | |
| **a** | 3.05-3.20 n=2 | 3.70-4.80 n=9 | 5.20-5.70 n=2 | - | - | - |
| **$a_1$** | 2.80 n=2 | 3.20-4.50 n=27 | 4.90-5.80 n=4 | 7.70 n=1 | 17.5 n=1 | 53.0-126.5 n=13 |
| **b** | 1.70-1.80 n=2 | 2.10-2.60 n=25 | 2.70-2.90 n=2 | 4.20 n=1 | - | 31.0-44.5 n=12 |
| **c** | 1.30-1.50 n=2 | 1.50-1.80 n=26 | 2.15-4.70 n=3 | - | - | - |
| **a / b** | 1.78-1.79 n=2 | 1.68-1.92 n=8 | 1.93 n=1 | - | - | - |
| **$a_1$/ b** | 1.56-1.65 n=2 | 1.50-1.73 n=20 | 1.81 n=1 | 1.83 n=1 | - | 2.34-2.96 n=12 |
| **$a_1$ / c** | 1.87-2.15 n=2 | 2.19-2.56 n=22 | 1.23-2.28 n=2 | - | - | - |

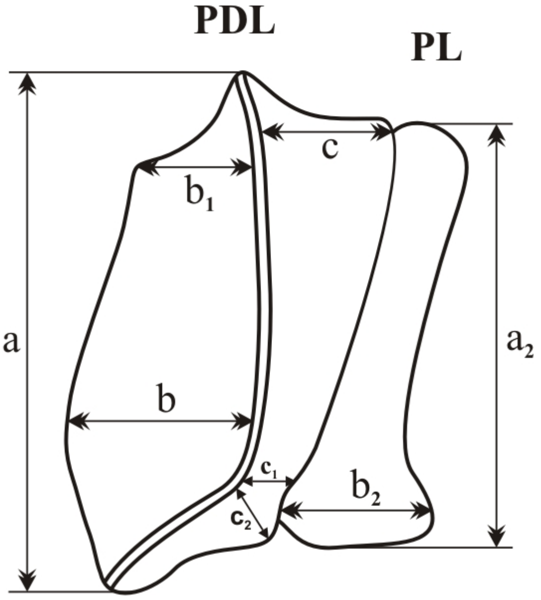
## 2.14. ADL (juvenile)



### **2.15. Posterior dorso lateral plate (PDL)** – for juveniles

| Length (a), width ($b$-$b_1$), high (c), mm | Juveniles of *Asterolepis ornata*, stage of ontogeny | |
|---|---|---|
| | 1-2 | 2 |
| **a** | 4.15 n=1 | 4.20-6.00 n=25 |
| **b** | 1.50 n=1 | 1.50-2.30 n=25 |
| $\mathbf{b_1}$ | 0.90 n=1 | 0.90-1.45 n=24 |
| **c** | 0.80 n=1 | 0.85-1.35 n=23 |
| $\mathbf{c_1}$ | 0.30 n=1 | 0.35-0.50 n=22 |
| $\mathbf{c_2}$ | 0.60 n=1 | 0.65-0.80 n=17 |
| **a / b** | 2.77 n=1 | 2.58-2.97 n=23 |
| $\mathbf{b / b_1}$ | 1.67 n=1 | 1.60-2.00 n=22 |
| $\mathbf{c / c_1}$ | 2.67 n=1 | 2.00-2.75 n=21 |

### **2.15., 2.16. PDL plus PL** – for juveniles

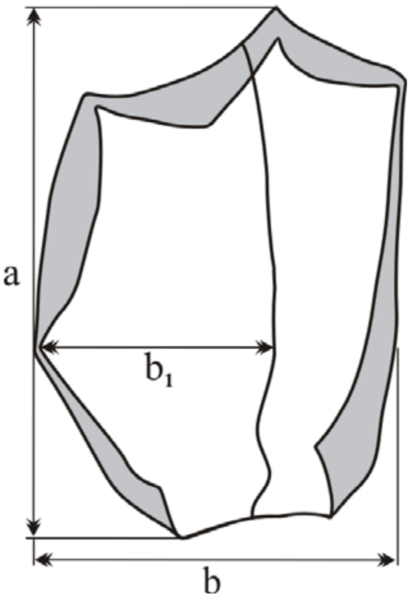


### **2.16. Posterior lateral plate (PL)**

| Length ($a_2$), width ($b_2$), mm | Juveniles of *Asterolepis ornata*, stage of ontogeny | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| $\mathbf{a_2}$ | - | 3.60-5.00 n=4 | 6.30-6.60 n=2 | - |
| $\mathbf{b_2}$ | - | 1.20-1.70 n=5 | 2.00-2.30 n=2 | - |
| $\mathbf{a_2 / b}$ | - | 2.74-3.08 n=4 | 2.74 n=1 | - |

## **2.17. Mixi-lateral plate (MxL)** – for adults

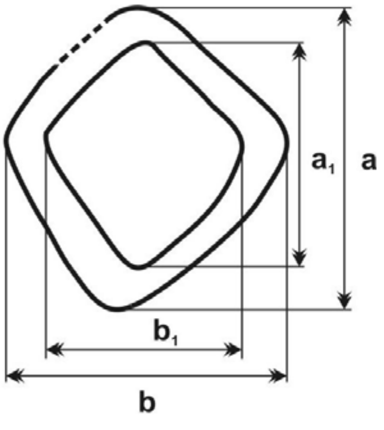
| Length (a), width (b-$b_1$), mm | *Asterolepis ornata* | |
|---|---|---|
| | Subadult | Adult |
| **a** | 40.6 n=1 | 118.2-163.0 n=8 |
| **b** | 17.5 n=1 | 30.9-67.5 n=17 |
| **$b_1$** | 8.0 n=1 | 18.2-38.5 n=16 |
| **a / b** | 2.32 n=1 | 2.19-2.66 n=8 |
| **b / $b_1$** | 2.19 n=1 | 1.35-2.14 n=16 |



## **2.18. Medio ventral plate (MV)**

| Length (a-$a_1$), width (b-$b_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | - | 2.20 n=1 | 2.60-3.20 n=2 | - | 54.0-82.0 n=2 |
| **$a_1$** | - | - | 2.30-2.40 n=2 | - | 35.0-70.0 n=4 |
| **b** | - | 1.60 n=1 | 2.40-2.90 n=2 | - | 48.0-76.0 n=2 |
| **$b_1$** | - | - | 1.80-2.00 n=2 | - | 35.0-66.8 n=4 |
| **a / b** | - | 1.38 n=1 | 0.97-1.10 n=2 | - | 1.08-1.13 n=2 |
| **$a_1$ / $b_1$** | - | - | 1.15-1.33 n=2 | - | 1.00-1.07 n=4 |

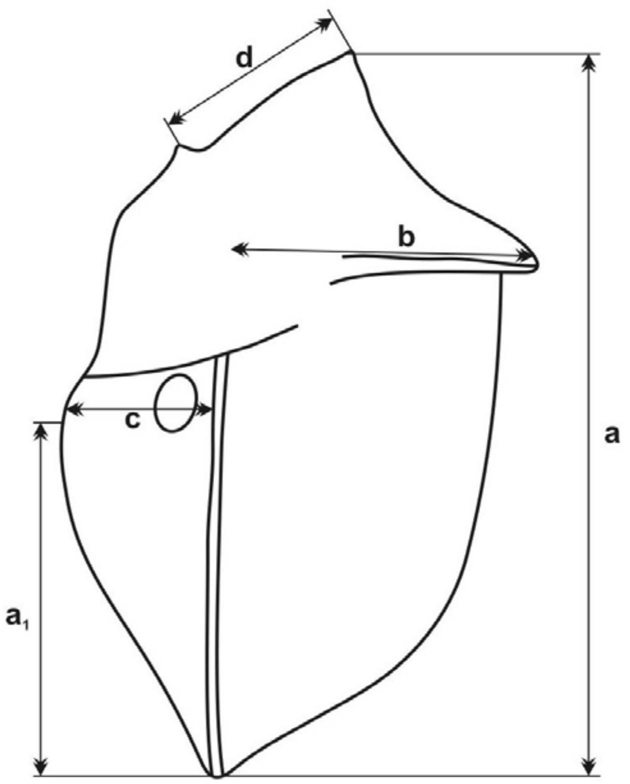
## **2.18. MV** (juvenile)



## 2.19. Anterior ventro lateral plate (AVL)

| Length (a-$a_1$,d), width (b), high (c), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 4 | |
| **a** | 5.50-6.10 n=3 | 6.30-8.70 n=34 | 8.90-11.40 n=8 | - | 78.0-148.0 n=3 |
| **$a_1$** | 3.10 n=1 | 3.30-3.70 n=16 | 3.60-5.40 n=5 | - | - |
| **b** | 2.00-2.30 n=3 | 2.50-4.00 n=31 | 3.80-5.00 n=7 | - | 40.0-84.9 n=3 |
| **c** | 1.80-2.00 n=2 | 1.80-2.20 n=25 | 1.90-2.80 n=6 | - | 23.0-32.0 n=2 |
| **d** | 1.70 n=1 | 1.50-1.80 n=24 | 1.80-2.60 n=5 | - | - |
| **a / b** | 2.18-2.75 n=3 | 2.05-2.38 n=25 | 2.09-2.28 n=5 | - | 1.54-1.99 n=3 |
| **a / $a_1$** | 1.77 n=1 | 1.91-2.36 n=16 | 1.98-2.29 n=4 | - | - |

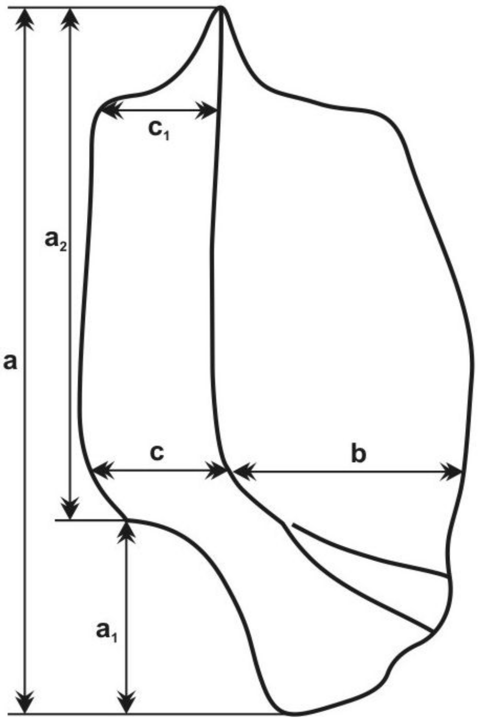
**2.19. AVL** (juvenile)



## 2.20. Posterior ventro lateral plate (PVL)

| Length ($a$-$a_2$), width ($b$), high ($c$-$c_1$), mm | Stages of ontogeny of *Asterolepis ornata* | | | | |
|---|---|---|---|---|---|
| | Juveniles | | | | Adult |
| | 1 | 2 | 3 | 3-4 | |
| **a** | 4.35-5.30 n=2 | 5.70-6.60 n=14 | 7.20-8.60 n=5 | 10.00-10.50 n=3 | 111.0-143.5 n=4 |
| **$a_1$** | 1.05-1.80 n=2 | 2.00-2.20 n=9 | 2.40-3.10 n=4 | 1.80 n=1 | - |
| **$a_2$** | 3.30-3.50 n=2 | 3.70-4.20 n=10 | 5.00-5.80 n=4 | - | - |
| **b** | 1.05-1.45 n=2 | 1.80-2.60 n=16 | 2.80-3.90 n=4 | 3.95-4.20 n=2 | 61.0-81.0 n=4 |
| **c** | 1.30 n=1 | 1.10-1.50 n=14 | 1.80-2.15 n=5 | 2.50 n=2 | 39.8-41.0 n=2 |
| **$c_1$** | 0.30 n=1 | 0.90-1.10 n=11 | 1.20-1.60 n=4 | 1.40-1.50 n=2 | - |
| **a / b** | 4.14 n=1 | 2.50-3.33 n=11 | 2.56-2.79 n=3 | 2.58 n=1 | 1.73-1.82 n=2 |
| **a/c** | 3.35 n=1 | 5.45-4.46 n=10 | 4.56-4.00 n=5 | 4.08 n=1 | 3.61-3.41 n=2 |
| **$a / a_1$** | 4.14-2.94 n=2 | 3.33-2.66 n=11 | 3.27-3.07 n=5 | - | - |
| **$a_2 / a_1$** | 3.14 n=1 | 1.66-2.33 n=9 | 1.68-2.27 n=4 | - | - |
| **$c / c_1$** | 4.33 n=1 | 1.16-1.50 n=10 | 1.38-1.50 n=2 | 1.67-1.79 n=2 | - |

## 2.20. PVL (juvenile)



# 3. List of tables and figures

## Tables

**Table 1.1.** List of animal and plant taxa recovered from the Lode pit, Lode Fm. (Upeniece, 2001, Table 1).

**Table 1.2.** Comparison of the Gauja Regional Stage vertebrates with those from the Upper Givetian and lowermost Frasnian formations of the Main Devonian Field, lowermost/Middle Frasnian of Miguasha and the Upper Givetian of Scotland and Timan correspondingly to the placoderm zonation of the Main Devonian Field (Upeniece, 2001, Table 2, with modifications) (after Ahlberg et al., 1999; Cloutier et al., 1996; Dineley, Loeffler, 1993; Esin et al., 2000; Ivanov, Lukševičs, 1996; Schultze, Cloutier, 1996; Valiukevičius, 1998).

**Table 3.1.** Disintegration stages of skeleton of adult placoderm *Asterolepis ornata* of various types of taphocoenoses in the Liepa (Lode) pit.

**Table 3.2.** Types of the taphocoenoses correlated to the lithology of the Gauja Regional Stage and paleoenvironment of burial in the deltaic regions.

**Table 3.3.** A comparison of organism assemblages of the Lode and Gauja Formations (Kuršs *et al*., 1999, Table 1, with modifications).

**Table 4.1.** Comparison of the proportions of *Asterolepis ornata* body in juveniles and adults (Upeniece, Upenieks, 1992, Table 1, with modifications).

**Table 4.2.** Measurements and indices of the median ventral (MV) plate in juveniles and adults of *Asterolepis ornata*.

**Table 4.3.** Ontogenetic stages of the early development of the dermal armour of juveniles of *Asterolepis ornata*.

**Table 5.1.** Proportions of *Lodeacanthus gaujicus* compared with those of members of Mesacanthidae and Acanthodidae (Upeniece, 1996, Table 1).

**Table 5.2.** Summary of preserved skeletal elements of *Lodeacanthus gaujicus*.

**Table 5.3.** The development of the squamation extent in acanthodian *Lodeacanthus gaujicus* (Upeniece, 1996, Table 2 with modifications).

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## Figures

**Fig. 1.1.** Palaeogeographical map of the Devonian terrigenous sedimentary basin for the late Givetian (Burtnieki Regional Stage) and early Frasnian (Gauja Regional Stage) in the East Baltic (V.Kuršs, 1992 a, Fig. 37 c). The Lode Formation stretches along the paleoslope for a distance between Lode and Pechory (Petseri).

**Fig. 1.2.** Peculiar section of deposits of the Lode (D ld) and Sietiņi (D st) formations in the Lode pit (1990). Slump processes resulted in deformations and even vertical orientation of beds. Section is semicircular as it follows the clay pit walls; the length of the section is 100 m. Colours approximately correspond to the colouration of rocks.

**Fig. 1.3.** "Juvenile fish" clay lense interbedded within the sandstones in the Lode clay pit (after Kuršs, in: Upeniece, Upenieks, 1992, Fig. 1). **1**, clay (mostly greenish-grey), with rare fish fragments and plant macrofossils; **2**, silty clay (mostly multicoloured); **3**, multicoloured gravelstone-clayey pebbles with clayey-silt cement; **4**, massive and cross bedded fine-grained sandstone; **5**, layers with numerous finds of Mysidaceans; **6**,

complete specimens of *Asterolepis ornata*; **7**, separate fish bones; **8**, juveniles and small fishes: a, complete individuals; b, separate armour plates; **9**, sulfide nodules.

**Fig. 3.1.** Detailed biostratigraphical section of the ”juvenile fish” lens. Liepa (Lode) clay pit, Latvia; lower Frasnian (Upeniece, 2001 b, Fig.2).

**Fig. 3.2.** Fossil circlets of parasitic platyhelminths hooks (marked with ellipses in A) inside the acanthodian *Lodeacanthus gaujicus*. A, LDM 270/18c (Upeniece, 2001b, Pl. 3, fig. 2); B, LDM 270/33a. Upper Devonian, Liepa (Lode) pit.

**Fig. 3.3.** Fossil hooks of parasitic platyhelminths. **A,** found in juvenile acanthodian body near the scapula (see also Fig. 3.5. No 17), LDM 270/4a. **B,** found near conchostracan. Upper Devonian, Liepa (Lode) pit.

**Fig. 3.4.** Localization areas of remains of parasitic platyhelminths. **A,** in placoderm juveniles of *Asterolepis ornata*. **B,** in juvenile and adult acanthodian *Lodeacanthus gaujicus*. Red circles – possible endoparasites, green circles – possible ectoparasites.

**Fig. 3.5.** Circlets of fossil hooks found in juveniles of placoderm fish *Asterolepis ornate* (No 1-11), in juveniles and adults of acanthodian *Lodeacanthus gaujicus* (No 12-23), and in/on crustacean Mysidacea (No 24) (Upeniece, 1999 a, Fig. 1).

**Fig. 3.6.** Recent parasitic flatworms. **A,B,** *Neodactylogyrus crucifera* (Monogenoidea) life style (Kearn, 1968, fig. 17): **A,** the early skin-parasitic larva. **B,** the gill-parasitic adult on the host (roach). C, larva of *Gyrocotyle urna*; e – embrional hooks (Ruszkowski, 1932).

**Fig. 3.7.** Distribution of adult placoderm *Asterolepis ornata* individuals in one of the largest accumulations in the Liepa (Lode) clay pit. Bodies without dotted central part indicate the pulled out AMD plates (presumably due to the internal pressure of decomposition gases in decaying armour) (Upeniece, 1999, Fig.1).

**Fig. 3.8.** Disarticulated skeleton of placoderm antiarch *Bothriolepis canadensis.* Head and trunk armour. AMD is absent and pulled off due to decomposition gases, specimen P2773b, dorsal side. Upper Devonian, Canada, Miguasha, Scaumenac Bay; haused in Stockholm Museum of Natural History.

**Fig. 3.9.** The distribution of fish remains in the fourth type of taphocoenosis (Kuršs *et al*. 1999, Fig.1). The remains of sarcopterygian *Laccognathus panderi* dominate this taphocoenosis. ADL, fragment of the anterior dorsal lateral plate of placoderm *Asterolepis ornata*.

**Fig. 3.10.** Proposed trophic relations within the Lode organism assemblage (# - infested by parasites).

**Fig. 4.1.** Two completely preserved juveniles of *Asterolepis ornata*. Mainly the visceral view of the dorsal wall exposed. Upper Devonian, Lode Formation, Liepa (Lode) clay pit, Latvia. **A,** LDM 260/223. **B,** LDM 260/224.

**Fig. 4.2.** Head shield of juvenile of *Asterolepis ornata* from the Liepa (Lode) pit: **A,** LDM 260/266a, in visceral view. **B,** LDM 260/266a,b, drawn on part and counterpart.

**Fig. 4.3. A, B**, Reconstruction of adult *Asterolepis ornata* (Lyarskaya, 1981, Fig. 74, with slight modifications in semilunar area). A, dorsal side, B, ventral side. **C, D**, Reconstruction of juvenile *Asterolepis ornata* (Upeniece, Upenieks, 1992, Figs. 2B, 3B). Grey solid lines indicate ridge system. C, dorsal side, D, ventral side.

**Fig. 4.4.** Reconstruction of juvenile of *Asterolepis ornata*. The 2nd stage of ontogeny. Grey solid lines indicate the ridge system. Mainly based on the specimen LDM 260/87, part and counterpart (see Fig. 4.18.). **A,** dorsal side. **B**, ventral side. Anatomical abbreviations in the appendix No 1.

**Fig. 4.5.** Juvenile individual of *Asterolepis ornata* LDM 260/13a, visceral view of the dorsal wall. Upper Devonian, Frasnian, Lode Fm., Latvia, Liepa (Lode) pit.

**Fig. 4.6.** Ridge system of juvenile *Asterolepis ornata*. Grey lines designate those of the head-shield and dorsal wall of the trunk armour; black lines designate those of the ventral wall of the trunk armour. Abbreviations in appendices No 1.

**Fig. 4.7.** Premedian plate (Prm) of *Asterolepis ornata*. **A**, of juvenile individual, LDM 260/374a. **B**, of adult individual (Gross, 1931, Pl. IV, Fig. 9).

**Fig. 4.8.** Dermal bones of the orbito-nasal cavity of juveniles and adults of *Asterolepis ornata* **A, B** Pineal plate (Pi) of juvenile. A, LDM 260/152a, in visceral view. B, LDM 260/118a, in visceral view. **C**, Pineal plate (Pi) of adult (Lukševičs, 2001, Fig. 3E), in external view. **D-E,** Rostral plate (R) of juvenile LDM 260/59a, in visceral view. **F**, Orbito-nasal cavity of juvenile. LDM 260/266a, in visceral view. **G**, Rostral plate (R) of adult (Lukševičs, 2001b, Fig. 5A), in external view. **H**, Orbito-nasal cavity of adult. UP 10/1-1.

**Fig. 4.9.** Dermal armour plates of the head-shields of juvenile *Asterolepis ornata* (**A-E**). A, LDM 260/82a, in visceral view. B, LDM 260/150a, in visceral view. C, LDM 260/152a, in visceral view. D, LDM 260/299a, in visceral view. E, The orbito-nasal cavity and adjacent plates of the advanced juvenile, LDM 260/78, in dorsal view. **F**, Armour plates of the head of adult *Asterolepis ornata* UP 10/1-1, in dorsal view.

**Fig. 4.10.** Sclerotic bones (Sclr) of the eyeball of juvenile *Asterolepis ornata*. A, LDM 260/403, in visceral view. B, C, LDM 260/87a, in visceral view.

**Fig. 4.11.** Postpineal plates (Pp) of *Asterolepis ornata*. **A-C**, of juveniles. A, LDM 260/87b, in dorsal view. B, LDM 260/299. C, LDM 260/152a, in visceral view. **D**, of adult (Karatajūte-Talimaa, 1963, Fig. 23-2).

**Fig. 4.12.** Sequence of development of nuchal plates (Nu) of *Asterolepis ornata* in juveniles **(A-G)**, and in subadults and adults **(H-L)**. A, B, the 1st stage of ontogeny, Nu in dorsal view. LDM 260/383b. C, D, the 2nd stage of ontogeny, Nu in dorsal view. LDM 260/385a. E, F, the 3rd stage of ontogeny, Nu in visceral view. LDM 260/150. G, the 3rd stage of ontogeny, Nu in visceral view. LDM 260/260. **H-I,** nuchal plate and adjacent armour plates of subadult individual, dorsal side. LDM 43/450. **J-L,** nuchal plates of adult individuals, in dorsal view. J, after Gross (1931, Pl. IV, fig. 6). K, unnumbered specimen LDM. L, posterior part of the nuchal plate. UP 10/1-1.

**Fig. 4.13.** Paranuchal plate (Pn) of *Asterolepis ornata.* **A, B**, of juvenile, left Pn, in dorsal view. A, LDM 260/266. B, LDM 260/193. **C**, **D**, of subadult, left Pn LDM 43/450, in dorsal view. River Gauja, outcrop Katlapi. **E, F**, of adult, right Pn. E, LDM 43/362, in dorsal view. River Gauja, outcrop Ērmaņi. F, after Gross (1931, Pl. IV, Fig. 5).

**Fig. 4.14.** Lateral plates (La) of *Asterolepis ornata*. **A-G**, of juvenile individuals. A, Left La, LDM 260/87b, in dorsal view. B, F, Left La, LDM 260/382a, in dorsal view. C, Left La, LDM 260/193. D, Attachment area to the SM plate, LDM 260/299a, in visceral view (fragment from Fig. 4.9.D). E, Right La, LDM 260/87a, in visceral view. G, Right La, LDM 260/374b, in dorsal view. **H**, of adult (after Gross, 1931, Pl. IV, Fig. 15).

**Fig. 4.15.** Postmarginal plate (Pmg) of *Asterolepis ornata.* **A, B,** of juvenile, right Pmg, LDM 260/152b, in dorsal view. **C,** of adult, left Pmg (Gross, 1931, Pl. IV, Fig. 2), in dorsal view.

**Fig. 4.16.** Right submarginal plate (SM) of juvenile of *Asterolepis ornata.* A, LDM 260/259a, in dorsal view. B, LDM 260/393.

**Fig. 4.17.** Suborbital (SO) and semilunar (Sm) plates of *Asterolepis ornata*. **A-C**, of juvenile individuals. A, a pair of SO bones, LDM 260/100a. B, right SO, LDM 260/402a, in visceral view. **C**, a pair of SO bones in upside-down position in visceral view; a pair of Sm plates in external view. LDM 260/1. **D,** a pair of SO and Sm bones of adult individual. UP 10/1-1, in external view. **E**, a pair of SO bones of the same individual.

**Fig. 4.18.** Disarticulated juvenile individual of *Asterolepis ornata* LDM 260/87a. Ventral wall of the trunk with detached armour plates from the dorsal side. This specimen mainly was used for the reconstruction.

**Fig. 4.19.** Reconstruction of juvenile of *Asterolepis ornata*, the 2nd stage of ontogeny, in lateral view (without pectoral fins). Grey solid lines indicate the ridge system.

**Fig. 4.20.** Contact area between the lateral plates ADL and AVL of juvenile of *Asterolepis ornata*, showing lateral fontanel on the lateral wall. Reconstruction of part and a counterpart. UP 10/2-4a,b.

**Fig. 4.21.** Anterior median dorsal (AMD) plate of *Asterolepis ornata*. **A-D**, of juveniles. A, B, in visceral view. Double lines indicate the grooves corresponding to the dorsal median ridge (dmr) and oblique transverse ridge (otr). LDM 260/248. C, in visceral view, LDM 260/363. D, in visceral view, advanced juvenile in about 5th stage of ontogeny, LDM 260/351. **E**, of subadult, in dorsal view. UP 10/1-7. **F**, of adult, in visceral view. UP 10/1-3.

**Fig. 4.22.** Posterior median dorsal plate (PMD) of *Asterolepis ornata*. **A, B,** of juvenile. Lode pit, Lode Fm. A, in visceral view. Double lines indicate the grooves corresponding to the dorsal median ridge (dmr) and to dorsal lateral ridge (dlr). LDM 260/526. B, of advanced juvenile, the 4th ontogenetic stage, LDM 260/529, in dorsal view. **C, D,** of adult. Sigulda town, Gauja Fm. C, (Karatajūte-Talimaa, 1963, Pl. VI, Fig. 3). D, (Karatajūte-Talimaa, 1963, Pl. VII, Fig. 1).

**Fig. 4.23.** Sequence of developmental stages of the anterior dorso-lateral plate (ADL) of *Asterolepis ornata*. **A-E**, left ADL of juvenile. Lode pit, Lode Fm. A, the 1st stage of ontogeny, LDM 260/200, in dorsal view. B, the 2nd stage of ontogeny, LDM 260/410, in dorsal view. C, the 2nd stage of ontogeny, Double lines indicate the grooves corresponding to the dorsal lateral ridge (dlr) and oblique transverse ridge (otr). LDM 260/87a,b, in visceral view. D, E, the 3rd stage of ontogeny, LDM 260/252a, in external view (D, drawn from a part and a counterpart). **F**, right ADL of adult, (Karatajūte-Talimaa, 1963, Fig. 34), in dorsal view. Ķūķu Cliff, Gauja Fm.

**Fig. 4.24. A-F**. Sequence of developmental stages of the posterior dorso-lateral plate (PDL) and posterior lateral plate (PL) of juvenile *Asterolepis ornata*. Lode pit, Lode Fm. A, left PDL, LDM 260/437ab, in dorsal view; B, left PDL, LDM 260/440ab, in dorsal view. C, right PDL plus PL, LDM 260/87ab, in dorsal view. D, E right PDL plus PL, LDM 260/241ab, in visceral view. Double lines indicate the grooves corresponding to dorsolateral ridge (dlr). F, right PL, LDM 260/152a, in dorsal view. **G**, **H**, left MxL plate of small individual of *Asterolepis ornata*, in dorsal view. Ķūķi Cliff, Gauja Fm. G, after Karatajūte-Talimaa (1963, Pl. V, Fig. 3). H, after Lyarskaya (1981, Fig. 84-2), in dorsal view. **I, J**, left MxL plate of adult individual, UP 10/1-4, in dorsal view. Lode pit, Lode Fm.

**Fig. 4.25.** The right anterior ventro-lateral plate (AVL) of juvenile of *Asterolepis ornata*. A, B, the 1st stage of ontogeny. LDM 260/458, in visceral view. Double lines indicate the grooves corresponding to the ventrolateral ridge (vlr) and the anterior transverse ventral ridge (atvr). C, D, the 2nd stage of ontogeny. C, LDM 260/250a, in external view. D, LDM 260/248b, in visceral view.

**Fig. 4.26.** Anterior ventro-lateral plate (AVL). **A, B**, juvenile of *Asterolepis ornata*. The 2nd stage of ontogeny. LDM 260/476a,b, in external view. A, ventral and lateral lamina, mirror image; B, lateral lamina. **C, D**, adult of *Asterolepis ornata*, in external view (Karatajūte-Talimaa, 1963, Fig. 54), Upper Devonian, Latvia; C, ventral and lateral lamina; D, lateral lamina. **E, F**, adult of *Bothriolepis canadensis,* in external view. Upper Devonian, Canada; E, ventral and lateral lamina (Stensiö, 1948, Fig. 166 D), F, lateral

lamina (Stensiö, 1959, Fig. 20 A). **G**, adult of *Remigolepis zhongningensis*, ventral lamina, in external view. Upper Devonian, China (Jiang *et al*., 1987, Fig. 29).

**Fig. 4.27.** Sequence of developmental stages of posterior ventro-lateral plate (PVL) of juveniles of *Asterolepis ornata*. **A,** left PVL, the 1st stage of ontogeny, mirror image, LDM 260/501, in external view. **B,** right PVL, the 2nd stage of ontogeny, LDM 260/502, in external view. **C,** right PVL, the 3rd stage of ontogeny, LDM 260/515, in external view. **D,** E right PVL, the 3rd stage of ontogeny, LDM 260/152, in external view (D-drawn from a part and a counterpart).

**Fig. 4.28. A-D**, Sequence of developmental stages of the median ventral (MV) plate of juveniles of *Asterolepis ornata*. **A,** ventral wall with ventral fontanel, a part and a counterpart. LDM 260/7ab, in visceral view (Upeniece, Upenieks, 1992, Pl.1, fig. 1). **B,** anterior part of the ventral wall; MV is initially developed, translucent, without ornamentation and roundish, LDM 260/237a, in visceral view. **C,** fragment of the MV plate; translucent, without ornamentation, LDM 260/94a, in visceral view. **D,** MV plate with developed ornamented and overlapped areas, LDM 260/153b. **E**, MV plate of adult of *Asterolepis ornata*, LDM G 291/89, in external view.

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**Fig. 4.30.** Pectoral fin plates of *Asterolepis ornata* with preserved serratiform sutural connections: of juvenile individuals (**A-D**), of adult (**E, F**). A, B, ventral central plate 1 ($Cv_1$), in visceral view. LDM 260/152b. C, D, mesial marginal plate 2 ($Mm_2$), in visceral view. LDM 260/152a. E, F, lateral marginal plate 3 ($Ml_3$), in external view. UP 10/1-6.

**Fig. 4.31. A-C.** Pectoral fin of juvenile *Asterolepis ornata*. A, B, LDM 260/301a, in external view. C, LDM 260/222b, in visceral view. **D, E**. Distal segment of the pectoral fin of adult *Asterolepis ornata*. D, after Gross (1931, Pl. VI, Fig. 3). E, UP 10/1-2. Lode pit. **F**, Pectoral fin of adult *Pterichthyodes milleri,* Middle Devonian, Scotland (Hemmings, 1978, fig. 18 A).

**Fig. 4.32.** Types of sutural connections between the head-shield plates of *Asterolepis ornata*. **A-E**, Serrated connection type in juvenile individuals, in external view. A, B, detached head plates LDM 260/5. C, detached head plates LDM 260/193. D, E, nuchal plate LDM 260/250. **F, G**, Oblique serratiform suture of adult. Pineal plate, in visceral view, with some preserved denticles. LDM 43/538.

**Fig. 4.33.** Types of sutural connections between the armour plates of *Asterolepis ornata*. Green lines indicate serratiform connections (of pectoral fins and partly of the head-shield), red lines – connections of squamous (overlapped) type (dorsal and ventral walls of the trunk armour). **A,** adult (after Lyarskaya, 1981, Fig. 74, with slight modifications in semilunar area). **B**, juvenile (Upeniece, Upenieks, 1992, Figs. 2B, 3B, with slight modifications in semilunar area).

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**Fig. 4.35.** Squamous part of juvenile *Asterolepis ornata*. **A,** with preserved dorsal fin. LDM 260/80a, in visceral view (scales with tubercle are in external view) (Upeniece, Upenieks, 1992, Pl.4, fig. 4). **B,** LDM 260/235a, in visceral view. Fulcral scales are shown in detail. **C,** LDM 260/88a, in visceral view. Flank scales are shown in detail. **D, E,** LDM 260/9. **E,** unknown symmetrical element.

**Fig. 4.36.** Scales of some placoderm fish, (**A-E,H-J**) and of thelodonts (**F-G**). **A**, *Stensioella heintzi*, flank scale, in external view. Lower Devonian, Germany (Gross, 1962, fig. 6 B,G). **B**, *Pterichthyodes milleri*, flank scale, in external view. Middle Devonian, Scotland (Hemmings, 1978, Fig. 22 C). **C**, Yunnanolepididae, flank scale, in external and visceral views after Ivanov et al., 1996, Fig. 8 I, M. Lower Devonian, China (Wang, 1991, fragment of Pl.1 A). **D,E,H-J, *Asterolepis ornata,*** Upper Devonian, Latvia, Lode pit. **D, H-J, of juvenile**. **D**, flank scales, in external and visceral views (Ivanov et al., 1996, Fig. 8 I, M). **H-I,** raw of fulcral scales in visceral view. **H,** with patch of flank scales in external view (on the right side), LDM 260/9 (Upeniece, Upenieks, 1992, fig.4). **I,** LDM 260/9. **J,** flank scales (Ivanov et al., 1996, Fig. 8 L). **E**, **scale of adult**, UP 10/1-5. **F, G,** scales of thelodont *Gampsolepis insueta.*

**Fig. 4.37.** The caudal part with dorsal fin of the small-sized yunnanolepid antiarch *Parayunnanolepis xitunensis*. Lower Devonian, China, Yunnan province. Specimen V 11679.1 (holotype), housed in Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China.

**Fig. 4.38.** Sequence of development of ornamentation of dermal bones in early growth stages in juveniles of *Asterolepis ornata.* **A**, Initial development of the fine-meshed network along the ridges of the ridge system. 1st ontogenetic stage. PVL plate LDM 260/500. **B**, Ornamentation of fine-meshed network covers the most area of the plate. Transition between the 1st and 2nd ontogenetic stage. AVL plate LDM 260/577. **C**, **D**, Fine-meshed ornamentation. 2nd ontogenetic stage. C, AVL plate LDM 260/489. D, ADL plate LDM 260/472. **E**, Transition between the 2nd and 3rd ontogenetic stage: fine-meshed ornamentation turns into the reticular one. AMD plate LDM 260/357. **F**, Reticular ornamentation. 3rd ontogenetic stage. PVL plate LDM 260/521. Scale bar 1 mm.

**Fig. 4.39.** Ornamentation of dermal bones in the advanced juveniles of *Asterolepis ornata.* **A**, Reticular ornament of radially anastomosing ridges. 4th ontogenetic stage. AMD plate LDM 260/539. **B**, Tubercular ornament of radially arranged tubercles in the points of union of anastomosing ridges. 5th ontogenetic stage. AMD plate LDM 260/78. **C**, Three types of ornamentation simultaneously presented on the plate: 1, fine-meshed, 2, reticular, 3, tubercular. AMD plate LDM 260/359. Scale bar 1 mm.

**Fig. 4.40.** Tubercular ornamentation of dermal bones of subadult (**A**) and of adult (**B**) individuals of *Asterolepis ornata*. Scale bar 1 mm.

**Fig. 4.41.** Juvenile individuals of *Asterolepis ornata* with the preserved fossilised stomach content (St); ventral view (external view of some dorsal trunk armours` plates). **A,** LDM 260/260. **B,** LDM 260/1.

**Fig. 4.42.** Trunk armour of small individual of antiarch *Pterichthyodes milleri*; inside view of the ventral wall with parts (B,C) of external surface of the dorsal wall. Middle Devonian, Scotland. **A**, specimen P4249 (housed in Swedish Museum of Natural History, Stockholm). **B**, fossilised stomach content (beneath the left ADL plate). **C**, reticular ornamentation on the PMD plate.

**Fig. 4.43.** The earliest known growth stages of juvenile individuals of *Asterolepis ornata*. The 1st stage of ontogeny. A, Disarticulated individual. LDM 260/200. B, Dorsal wall with detached AVL plate from the ventral wall. LDM 260/156. Upper Devonian, Liepa (Lode) pit, Latvia.

**Fig. 4.44.** Juvenile individuals of *Asterolepis ornata* with the well-preserved scale covering of the caudal part. The 2nd stage of ontogeny. A, Dorsal side. LDM 260/235b (Upeniece, 2001, Pl. 1, fig. 7). B, Ventral side. LDM 260/2a.

**Fig. 4.45.** Juvenile individuals of *Asterolepis ornata* belonging to the 3rd stage of ontogeny, in ventral view. A, LDM 260/118 (Upeniece, 2001, Pl.1, fig. 6). B, LDM 260/25.

**Fig. 4.46.** Juvenile individual of *Asterolepis ornata* in the 4th stage of ontogeny. The head-shield and anterior part of the dorsal trunk armour LDM 260/78.

**Fig. 4.47.** Incomplete juvenile individual of *Asterolepis ornata*. The 5th stage of ontogeny. Dorsal side. LDM 260/10.

**Fig. 5.1.** Completely squamated (presumably adult) individuals of acanthodian *Lodeacanthus gaujicus* Upeniece. **A**, LDM 270/19a (caudal part turned over); **B**, LDM 270/9a; C, LDM 270/7a.

**Fig. 5.2.** The smallest known acanthodian larval-juvenile individual of *Lodeacanthus gaujicus* without the squamation. It represents the smallest described until now whole-bodied acanthodian. The body is covered merely with a film of skin, the head is indicated only by the presence of an eye stain, and a few branchiostegal rays. Well-developed fin spines and scapula indicate a presence of an acanthodian individual. **A**, photo of specimen LDM 270/45 a; **B**, drawing from a part and counterpart: LDM 270/45 a, LDM 270/45 b.

**Fig. 5.3.** Reconstruction of mesacanthid *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 4, with slight modifications) and indicated distances: **as-caudal cleft**, distance from anal spine to caudal cleft; **as-ds**, distance between anal and dorsal spines; **diam**, outer diameter of circumorbital ring; **ds-caudal cleft**, distance from dorsal spine to caudal cleft; **ps-as**, distance between pectoral and anal spines; **ps-ds**, distance between pectoral and dorsal spines; **ps- posterior end**, distance from pectoral spine to tip of tail; **ps-is**, distance between pectoral and intermediate spines; **ps-pls**, distance between pectoral and pelvic spines. **Y** - number of scales per millimetre in a natural, oblique row (postdorsal-precaudal region).

**Fig. 5.4.** Schematic presentation of proportions of the body and the squamation extent (in yellow) of the most complete specimens of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig.3, with modifications). Red strips indicate well marked unsquamated region, covered by film of skin (above the black horizontal line - in the dorsal part, below - in the ventral part of the body). Vertical interrupted line divides all bodies into a prepectoral region (the head + gill chamber, to the left) and a trunk (to the right). Specimen numbers to the left. Values in parentheses mean the estimated total specimen length unlike the measured values. Approximate measurements denoted by asterik. Measurements in mm.

**Fig. 5.5.** Nasal bones of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1 E, F, G). **A, B**, with surrounding tesserae, specimen LDM 270/40a; **C**, a pair of bones, LDM 270/34b; **D**, detached bone, LDM 270/7a.

**Fig. 5.6.** Juvenile individual of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 2 A, Pl. 1, Fig. 3) LDM 270/12 (total length 23.0 mm). Squamation reaches endocranium (en), squamation extent 84 % (see also Fig. 5.4). Drawing compiled from part (LDM 270/12a) and counterpart (LDM 270/12b).

**Fig. 5.7.** **A**, Circumorbital ring of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1H) in visceral view, after part (LDM 270/2a) and counter part (LDM 270/2b). Thick lines = natural margins, thin lines = broken margins. Presumably six circumorbital bones are preserved. **B**, head of the same specimen, LDM 270/2b. Redish patches presumably are fragments of the neurocranium.

**Fig. 5.8.** Jaws of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig.1 B-D). **A,B**, upper jaws (palatoquadrates) of specimens LDM 270/29 and LDM 270/30; **C**, lower jaw (Meckelian cartilage), LDM 270/40.

**Fig. 5.9.** Articulation area of scapula and pectoral fin spine in *Lodeacantus gaujicus* (Upeniece, 1996, Fig. 1 J). Specimen LDM 270/18 a.

**Fig. 5.10.** Fragment of posthyoidean branchial arches of left side of *Lodeacanthus gaujicus*, lateral view. At least five pairs are present. Question mark points to unknown small bones. Specimen LDM 270/14. **A**, photo; **B**, drawing (Upeniece, 1996, Fig. 1 I).

**Fig. 5.11.** Schematic presentation of proportions of caudal part of squamated, incompletely preserved individuals of *Lodeacanthus gaujicus* (Upeniece, 1996, part of Fig. 3). A, LDM 270/11. B, LDM 270/13. C, LDM 270/10.

**Fig. 5.12.** Caudal fins of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 2 C, D, with slight modifications). **A**, Individual of presumably subadult-adult transition stage, LDM 270/11; **B**, presumably adult individual, LDM 270/13.

**Fig. 5.13.** Scales and tesserae of *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Fig. 1; Pl.1, figs.1-7; Pl. 2). Red circles indicate exact location of scales or tesserae. **A,B**, tesserae, specimen LDM 270/34c-1A; **C-E**, scales and section from the trunk zone, LDM 270/15a-2B; **F-H**, scales from the axial lobe, LDM 270/59-1c; I,J, scales from the trunk zone, LDM 270/55-1e; **K**, section of scale from the trunk zone, LDM 270/15a1B. Scale bar 0.1 mm.

**Fig. 5.14.** Squamation in *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Pl. 1, Figs. 8,9) of a trunk zone. **A, B**, specimen LDM 270/20. Scale bar 0.1 mm. (Both scanning electron microscope photoes by M.Sc. V.Mikli, Tallinn.)

**Fig. 5.15.** Zones of squamation in acanthodian *Lodeacanthus gaujicus* (Upeniece, Beznosov, 2002, Fig. 1,2, with modifications). **1**, dorsal surface of the head; **2**, cheek region; scales from specimens LDM 270/9a, LDM 270/38a; **3**, trunk scales; scales from LDM 270/9, LDM 270/39; **4**, ventral scales; scales from LDM 270/9, LDM 270/7a; **5**, pectoral fin scales; **6**, caudal fin: **6 a**, scales of the axial lobe; scale from LDM 270/9; **6 b**, scales of the hypochordal lobe.

**Fig. 5.16.** Two types of base of the scale in juvenile individual of *Lodeacanthus gaujicus*. Specimen LDM 270/12. **A, B**, complete fish, counterpart and part; **C-E**, enlarged areas, marked by rectangular areas on A, showing conical bases of scales from lateral zone (C) (presumably fully developed); incompletely developed bases of scales with a deep ventral pit from the ventral (D) and dorso-lateral area (E) of prepectoral region.

**Fig. 5.17.** Fragment of cheek region of *Lodeacantus gaujicus*, covered by enlarged scales (zone 2 in Fig. 5.15). Specimen LDM 270/38a.

**Fig. 5.18.** Head of incompletely squamated individual of *Lodeacanthus* LDM 270/46. Infraorbital sensory line is visible. **A**, LDM 270/46b; **B**, combined drawing of a part (LDM 270/46a) and a counterpart (LDM 270/46b).

**Fig. 5.19.** Histology of scales of *Lodeacantus gaujicus* (Upeniece, Beznosov, 2002, Plate 2). Scale of trunk zone. **A**, horizontal section through the crown, specimen LDM 270/15a-2B; **B**, vertical longitudinal section, LDM 270/15a-1B.

**Fig. 5.20.** Juvenile individual of *Lodeacanthus gaujicus* LDM 270/28. Squamation reaches the dorsal fin spine (ds). Film of skin covers the middle part of the trunk (Upeniece, 1996, Fig. 2 B). 16, number of scales per millimeter in a row. **A**, photo. **B**, drawing of the same specimen.

**Fig. 5.21.** Incompletely developed squamation of juvenile individuals of *Lodeacanthus gaujicus*. Squamation reaches diagonally forward to the level of the pelvic fin spines. The rest of the trunk is covered by the film of skin. Caudal part is to the right. **A**, specimen LDM 270/1b; **B**, LDM 270/44a.

**Fig. 5.22.** Presumably adult individual of *Lodeacanthus gaujicus* (Upeniece, 1996, Fig. 1 A), see also the squamation extent in Fig. 5.4. Holotype LDM 270/38. **A**, photo of LDM 270/38a; **B**, drawing of a part and counterpart: LDM 270/38a, LDM 270/38b.

**Fig. 5.23.** Sequence of development of the squamation and head elements in *Lodeacanthus gaujicus*. **A**, stage of development without squamation; **B-D**, incompletely developed squamation; **E**, completely developed squamation.

**Fig. 5.24.** Comparison of development of the squamation in Mesacanthidae **(A)** and Acanthodidae **(B-D)**: **A**, *Lodeacanthus gaujicus* Upeniece (Upeniece, 2011); **B**, *Acanthodes gracilis* Beyrich (Zajic, 2005, Fig. 23); **C**, *Acanthodes bridgei* Zidek (Zidek, 1976, Fig. 13); **D**, *Acanthodes bronni* Agassiz (Heidtke, 1990, Fig. 52).

**Fig. 5.25.** Changes of proportions between the prepectoral distance and the total length of the body during the growth.

**Fig. 5.26.** Changes of proportions of fin spines during the growth. **A**, between the intermediate (is) and anal fin spine (as); **B**, between the intermediate (is) and pectoral fin spine (ps); **C**, between the pelvic (pls) and pectoral fin spine (ps); **D**, between the pelvic (pls) and anal fin spine (as).

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**1.1. att.** Devona terigēnās sedimentācijas baseina paleoģeogrāfiskā karte Živetas (Burtnieku reģionālais stāvs) un Agrā Franas (Gaujas reģionālais stāvs) stāvam Baltijas austrumu daļā (V.Kuršs, 1992 a, fig. 37 c). Lodes svīta stiepjas gar paleonogāzi virzienā no Lodes līdz aptuveni Pečoriem (Petseri).

**1.2. att.** Lodes un Sietiņu svītas nogulumu savdabīgs griezums Lodes karjerā (1990.g.). Noslīdeņu procesi izraisīja deformācijas un pat vertikālu slāņu sagulumu. Griezuma garums 100 m; griezums ir pusloka formā sakarā ar karjera sienu izvietojumu. Krāsas aptuveni atbilst iežu dabīgajai krāsai.

**1.3. att.** “Zivju mazuļu” iegula smilšakmeņos (V.Kurša attēls, publicēts: Upeniece, Upenieks, 1992, Fig. 1). **1**, māli (pārsvarā zaļpelēki), ar retiem zivju atlieku un augu fragmentiem; **2**, aleirītiski māli (pārsvarā daudzkrāsaini); **3**, daudzkrāsaini māla oļi ar mālaini aleirītisku cementu; **4**, masīvi un slīpslāņaini smalkgraudaini smilšakmeņi; **5**, slānīši ar vēžveidīgo Mysidaceans atliekām; **6**, veseli bruņuzivju *Asterolepis ornata* skeleti; **7**, atsevišķi zivju kauli; **8**, zivju mazuļu un sīku zivju atliekas: a, veseli skeleti; b, atsevišķas bruņu plātnes; **9**, sulfīdu konkrēcijas.

**3.1. att.** “Zivju mazuļu” iegulas detalizēts ģeoloģiskais griezums. Liepas (Lodes) māla karjers, devons, Latvija (Upeniece, 2001 b, Fig.2.).

**3.2. att.** Fosilo parazītisko plakantārpu piestiprināšanās kāsīši (A attēlā - apvilkti ar elipsēm) akantodēs *Lodeacanthus gaujicus*. A, LDM 270/18c (Upeniece, 2001b, Pl. 3, fig. 2); B, LDM 270/33a. Augšdevons, Liepas (Lodes) karjers.

**3.3. att.** Fosilo parazītisko plakantārpu piestiprināšanās kāsīši. A, atrasts akantodes mazulī pie lāpstiņas kaula (sk. arī Fig. 3.5. Nr. 17), LDM 270/4a. **B,** atrasts pie lapkājvēzīša. Augšdevons, Liepas (Lodes) karjers.

**3.4. att.** Parazītisko plakantārpu lokalizācijas vietas: **A,** bruņuzivju *Asterolepis ornata* mazuļos. **B,** akantožu *Lodeacanthus gaujicus* mazuļos un pieaugušos īpatņos. Sarkanie aplīši – iespējamie endoparazīti, zaļie aplīši – iespējamie ektoparazīti.

**3.5. att.** Fosilo parazītisko tārpu atlieku – āķīšu atradumi bruņuzivju *Asterolepis ornata* mazuļu skeletos (Nr. 1-11), akantožu *Lodeacanthus gaujicus* mazuļu un pieaugušu īpatņu skeletos (Nr. 12-23), kā arī vienā šķeltkājvēzītī Mysidacea (Nr. 24) (Upeniece, 1999 a, 1.att.).

**3.6. att.** Mūsdienu parazītiskie plakantārpi. **A, B,** *Neodactylogyrus crucifera* (Monogenoidea) dzīves veids (Kearn, 1968): **A,** kāpurs uz zvīņojuma. **B,** pieaudzis parazīts starp raudas žaunu lapiņām. **C,** *Gyrocotyle urna* kāpurs; e – embrionālie kāši (Ruszkowski, 1932).

**3.7. att.** Pieaugušo bruņuzivju *Asterolepis ornata* izvietojums vienā no lielākajiem to sakopojumiem Liepas (Lodes) mālu karjerā. Brunuzivju ķermeņiem, kuriem ķermeņa centrālā daļa ir attēlota bez punktējuma, ir atdalījušās priekšējās muguras bruņu plātnes (AMD), domājams, trūdgāzu izdalīšanās rezultātā (Upeniece, 1999, Fig.1).

**3.8. att.** Bruņuzivs *Bothriolepis canadensis* daļēji saglabājies skelets. Galvas vairogs un rumpja bruņas ar ķermeņa trūdgāzu izdalīšanās rezultātā atrautu un klāt neesošu priekšējo vidējo muguras plātni (AMD); paraugs P2773b, dorsālā puse. Augšdevons, Kanāda, Miguaša. Stokholmas Dabas vēstures muzejs.

**3.9. att.** Zivju atlieku izplatība 4.tafocenožu tipā (Kuršs *et al.* 1999, Fig. 1). Tafocenozē dominē daivspurzivju *Laccognathus panderi* atliekas. ADL, bruņuzivs *Asterolepis ornata* priekšējā muguras-sānu bruņu plātne.

**3.10. att.** Iespējamās barības ķēdes Lodes organismu paleobiocenozē (# - ar parazītu atliekām).

**4.1. att.** Divi pilnīgi veseli saglabājušies bruņuzivju *Asterolepis ornata* mazuļu skeleti. Dorsālo sienu iekšskats. Augšdevons, Lodes svīta, Liepas (Lodes) mālu karjers, Latvija. **A**, LDM 260/223. **B**, LDM 260/224.

**4.2. att.** Bruņuzivs *Asterolepis ornata* mazuļa galvas vairogs. Liepas (Lodes) karjers. **A,** LDM 260/266a, iekšskats. **B,** LDM 260/266a,b, kombinēts zīmējums no abām parauga pusēm.

**4.3. att.** **A, B**, Pieaugušas bruņuzivs *Asterolepis ornata* rekonstrukcija (Lyarskaya, 1981, Fig. 74, ar nelielām izmaiņām semilunāres reģionā). A, mugurpuse. B, vēderpuse. **C, D**, Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija (Upeniece, Upenieks, 1992, Figs. 2B, 3B). Pelēkās līnijas iezīmē valnīšu sistēmu. C, mugurpuse. D, vēderpuse.

**4.4. att.** Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija. Otrā ontoģenētiskās attīstības stadija. Pelēkās līnijas iezīmē valnīšu sistēmu. Pārsvarā izmantotas parauga LDM 260/87a un 260/87b abas puses (sk. Fig. 4.18.). **A,** mugurpuse. **B**, vēderpuse. Apzīmējumu saraksts pielikumā Nr. 2.

**4.5. att.** Bruņuzivs *Asterolepis ornata* mazulis LDM 260/13a, galvas vairoga un muguras sienas bruņu plātņu iekšskats. Augšdevons, franas stāvs, Lodes svīta, Latvija, Liepas (Lodes) karjers.

**4.6. att.** Bruņuzivs *Asterolepis ornata* mazuļa valnīšu sistēma. Pelēkās līnijas ir galvas vairoga un rumpja dorsalās puses valnīšu sistēma; melnās līnijas – ventrālās puses valnīšu sistēma. Apzīmējumu saraksts pielikumā Nr. 1.

**4.7. att.** Bruņuzivs *Asterolepis ornata* priekšējais nepāra kauls (Prm). **A**, mazulim, LDM 260/374a. **B**, pieaugušam indivīdam (Gross, 1931, Pl. IV, Fig. 9).

**4.8. att.** Orbito-nazālā dobuma kompleksa kauli bruņuzivs *Asterolepis ornata* mazuļiem un pieaugušajiem īpatņiem. **A, B,** Pineālais kauls (Pi) mazulim. A, LDM 260/152a, iekšskats. B, LDM 260/118a, iekšskats. **C**, Pineālais kauls (Pi) pieaugušam īpatnim (Lukševičs, 2001, Fig. 3E), ārskats. **D-E,** Rostrālais kauls (R) mazulim LDM 260/59a, iekšskats. **F**, Orbito-nazālais dobums mazulim LDM 260/266a, iekšskats. **G**, Rostrālais kauls (R) pieaugušam īpatnim (Lukševičs, 2001b, Fig. 5A), ārskats. **H**, Orbito-nazālais dobums pieaugušam īpatnim. UP 10/1-1.

**4.9. att.** Bruņuzivs *Asterolepis ornata* mazuļa galvas vairoga dermālās bruņu plātnes (**A-E**). A, LDM 260/82a, iekšskats. B, LDM 260/150a, iekšskats. C, LDM 260/152a, iekšskats. D, LDM 260/299a, iekšskats. E, Orbito-nazālais dobums un blakus esošās galvas vairoga bruņu plātnes lielākam mazulim, LDM 260/78, dorsālais skats. **F**, Pieaugušas bruņuzivs *Asterolepis ornata* galvas bruņu plātnes UP 10/1-1, dorsālais skats.

**4.10. att.** Acs ābola sklerotiskie kauli (Sclr) bruņuzivs *Asterolepis ornata* mazulim. **A**, LDM 260/403, iekšskats. **B, C**, LDM 260/87a, iekšskats.

**4.11. att.** Bruņuzivs *Asterolepis ornata* pakaļējais pineālais kauls (Pp). **A-C**, mazuļiem. A, LDM 260/87b, dorsālais skats. B, LDM 260/299. C, LDM 260/152a, iekšskats. **D**, pieaugušam īpatnim (Karatajūte-Talimaa, 1963, Fig. 23-2).

**4.12. att.** Pakauša kaula (Nu) secīga attīstība bruņuzivju *Asterolepis ornata* mazuļiem **(A-G)**, pusaugu un pieaugušiem indivīdiem **(H-L)**. A, B, Pirmā ontoģenētiskās attīstības stadija, dorsālais skats. LDM 260/383b. C, D, Otrā ontoģenētiskās attīstības stadija, dorsālais skats. LDM 260/385a. E, F, Trešā ontoģenētiskās attīstības stadija, iekšskats. LDM 260/150. G, Trešā ontoģenētiskās attīstības stadija, iekšskats. LDM 260/260. **H-I,** pakauša kauls un apkārtējās bruņu plātnes pusaugu īpatnim, dorsālā puse. LDM 43/450. **J-L,** pakauša kauli pieaugušiem īpatņiem, dorsālais skats. J, pēc Gross (1931, Pl. IV, fig. 6). K, nenumurēts paraugs LDM. L, pakauša kaula aizmugurējā daļa. UP 10/1-1.

**4.13. att.** Bruņuzivs *Asterolepis ornata* sānu pakauša kauls (Pn). **A, B**, mazuļiem, kreisais Pn, dorsālais skats. A, LDM 260/266. B, LDM 260/193. **C**, **D**, pusaugu īpatņiem, kreisais Pn LDM 43/450, dorsālais skats. Gauja, Katlapi. **E, F**, pieaugušiem īpatņiem, labais Pn. E, LDM 43/362, dorsālais skats. Gauja, Ērmaņi. F, pēc Gross (1931, Pl. IV, Fig. 5).

**4.14. att.** Bruņuzivs *Asterolepis ornata* sānu plātnes (La). **A-G**, mazuļiem. A, kreisā La, LDM 260/87b, dorsālais skats. B, F, kreisā La, LDM 260/382a, dorsālais skats. C, kreisā La, LDM 260/193. D, piestiprināšanās vieta SM plātnei, LDM 260/299a, iekšskats (fragments no Fig. 4.9.D). E, labā La, LDM 260/87a, iekšskats. G, labā La, LDM 260/374b, dorsālais skats. **H**, pieaugušam īpatnim (pēc Gross, 1931, Pl. IV, Fig. 15).

**4.15. att.** Bruņuzivs *Asterolepis ornata* pakaļējās malas plātne (Pmg). **A, B,** mazuļiem, labā Pmg, LDM 260/152b, dorsālais skats. **C,** pieaugušam īpatnim, kreisā Pmg (Gross, 1931, Pl. IV, Fig. 2), dorsālais skats.

**4.16. att.** Bruņuzivs *Asterolepis ornata* mazuļa labais žaunu vāks (SM). A, LDM 260/259a, dorsālais skats. B, LDM 260/393.

**4.17. att.** Bruņuzivs *Asterolepis ornata* zemacu kauls (SO) un pusmēness kauls (Sm). **A-C**, mazuļiem. A, zemacu kaulu pāris (SO), LDM 260/100a. B, labais SO, LDM 260/402a, iekšskats. **C**, zemacu kaulu pāris (SO) in upside-down position, iekšskats; pusmēness kaulu pāris (Sm), ārskats. LDM 260/1. **D,** pieauguša īpatņa SO un Sm kaulu pāri. UP 10/1-1, ārskats. **E**, SO kaulu pāris iepriekšējam īpatnim.

**4.18. att.** Bruņuzivs *Asterolepis ornata* fragmentēts mazulis LDM 260/87a. Ķermeņa ventrālās sienas bruņu plātnes ar atsevišķām muguras un laterālo sieniņu bruņu plātnēm (AMD, ADL, PDL, PL). Pēc šī parauga gk. tika veikta rekonstrukcija.

**4.19. att.** Bruņuzivs *Asterolepis ornata* mazuļa rekonstrukcija, otrā ontoģenētiskās attīstības stadija, sānskats (bez krūšu peldspurām). Pelēkās līnijas iezīmē valnīšu sistēmu.

**4.20. att.** ADL un AVL bruņu plātņu kontaktējošais laukums bruņuzivs *Asterolepis ornata* mazulim, redzams sānu atvērums laterālajā sienā. Rekonstrukcija pēc abām parauga pusēm. UP 10/2-4a,b.

**4.21. att.** Bruņuzivs *Asterolepis ornata* priekšējā vidējā muguras plātne (AMD). **A-D**, mazuļiem. A, B, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-mediālam valnītim (dmr) un slīpam šķērseniskam valnītim (otr) dorsālajā pusē. LDM 260/248. C, iekšskats, LDM 260/363. D, piektā ontoģenētiskās attīstības stadija, iekšskats, LDM 260/351. **E**, pusaugu īpatnis, dorsālais skats. UP 10/1-7. **F**, pieaudzis īpatnis, iekšskats. UP 10/1-3.

**4.22. att.** Bruņuzivs *Asterolepis ornata* pakaļējā muguras plātne (PMD). **A, B,** mazuļiem. A, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-mediālam valnītim (dmr) un dorsāli-laterālajam valnītim (dlr). LDM 260/526. B, Ceturtā ontoģenētiskās attīstības stadija, LDM 260/529, dorsālais skats. **C, D,** pieaugušam īpatnim. Sigulda, Gaujas svīta. C, (Karatajūte-Talimaa, 1963, Pl. VI, Fig. 3). D, (Karatajūte-Talimaa, 1963, Pl. VII, Fig. 1).

**4.23. att.** Secīga attīstība priekšējai muguras-sānu plātnei (ADL) bruņuzivīm *Asterolepis ornata*. **A-E**, kreisā ADL mazuļiem. A, Pirmā ontoģenētiskās attīstības stadija. LDM 260/200, dorsālais skats. B, Otrā ontoģenētiskās attīstības stadija, LDM 260/410, dorsālais skats. C, Otrā ontoģenētiskās attīstības stadija. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-laterālajam valnītim (dlr) un slīpam šķērseniskam valnītim (otr). LDM 260/87a,b, iekšskats. D, E, Trešā ontoģenētiskās attīstības stadija, LDM 260/252a, ārskats (D, zīmēts no abām parauga pusītēm). **F**, labā ADL no pieauguša indivīda, (Karatajūte-Talimaa, 1963, Fig. 34), dorsālais skats. Ķūķu iezis, Gaujas svīta.

**4.24. att.** **A-F**. Secīga attīstība pakaļējai muguras-sānu plātnei (PDL) un pakaļējai-sānu plātnei (PL) bruņuzivju *Asterolepis ornata* mazuļiem. A, kreisā PDL, LDM

260/437ab, dorsālais skats; B, kreisā PDL, LDM 260/440ab, dorsālais skats. C, labā PDL plus PL, LDM 260/87ab, dorsālais skats. D, E labā PDL plus PL, LDM 260/241ab, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst dorsāli-laterālajam valnītim (dlr). F, right PL, LDM 260/152a, dorsālais skats. **G**, **H**, kreisā MxL plātne no neliela *Asterolepis ornata* īpatņa, dorsālais skats. Ķūķu iezis, Gaujas svīta. G, pēc Karatajūte-Talimaa (1963, Pl. V, Fig. 3). H, pēc Lyarskaya (1981, Fig. 84-2), dorsālais skats. **I, J**, kreisā MxL plātne no pieauguša īpatņa, UP 10/1-4, dorsālais skats. Lodes karjers, Lodes svīta.

**4.25. att.** Bruņuzivs *Asterolepis ornata* mazuļa priekšējā vēdera-sānu plātne (AVL). A, B, Pirmā ontoģenētiskās attīstības stadija. LDM 260/458, iekšskats. Dubultās līnijas norāda rievas visceralajā pusē, kas atbilst ventrāli-laterālajam un AVL plātnes priekšējam šķērseniskajam vēdera valnītim (atvr). C, D, Otrā ontoģenētiskās attīstības stadija. C, LDM 260/250a, ārskats. D, LDM 260/248b, iekšskats.

**4.26. att.** Priekšējā vēdera-sānu plātne (AVL). **A**, **B**, bruņuzivs *Asterolepis ornata* mazulim. Otrā ontoģenētiskās attīstības stadija. LDM 260/476a,b, ārskats. A, ventrālā un laterālā plakne, spoguļattēls; B, laterālā plakne. **C, D**, *Asterolepis ornata* pieaugušam īpatnim, ārskats (Karatajūte-Talimaa, 1963, Fig. 54), augšdevons, Latvija; C, ventrālā un laterālā plakne; D, laterālā plakne. **E, F**, bruņuzivs *Bothriolepis canadensis* pieaugušam īpatnim, ārskats. Augšdevons, Kanāda; E, ventrālā un laterālā plakne (Stensiö, 1948, Fig. 166 D), F, laterālā plakne (Stensiö, 1959, Fig. 20 A). **G**, bruņuzivs *Remigolepis zhongningensis* pieaugušam īpatnim, ventrālā plakne, ārskats. Augšdevons, Ķīna (Jiang *et al.*, 1987, Fig. 29).

**4.27. att.** Bruņuzivs *Asterolepis ornata* mazuļa pakaļējā vēdera-sānu kaula (PVL) attīstības stadijas. **A,** kreisais PVL, pirmā ontoģenētiskās attīstības stadija, spoguļattēls, LDM 260/501, ārskats. **B,** labais PVL, otrā ontoģenētiskās attīstības stadija, LDM 260/502, ārskats. **C,** labais PVL, trešā ontoģenētiskās attīstības stadija, LDM 260/515, ārskats. **D,** E labais PVL, trešā ontoģenētiskās attīstības stadija, LDM 260/152, ārskats (D-kombinēts zīmējums no abām parauga pusītēm).

**4.28. att. A-D**, Bruņuzivs *Asterolepis ornata* mazuļa vidējās ventrālās bruņu plātnes (MV) attīstības stadijas. **A**, vēdera sieniņa ar ventrālo atvērumu, abas parauga puses. LDM 260/7ab, iekšskats (Upeniece, Upenieks, 1992, Pl.1, fig. 1). **B**, vēdera sienas priekšējā daļa; MV plātne ir sākotnējā attīstības stadijā, caurspīdīga, bez ornamentējuma, ieapaļas formas, LDM 260/237a, iekšskats. **C**, MV plātnes fragments, bez ornamentējuma, LDM 260/94a, iekšskats. **D**, MV plātne ar attīstītu ornamentējumu un pārklājumu malām, LDM 260/153b. **E**, MV plātne pieaugušam īpatnim *Asterolepis ornata*, LDM G 291/89, ārskats.

**4.29. att.** Pusmēness kauls (Sm). **A, B** bruņuzivs mazulim *Asterolepis ornata.* A, LDM 260/239, iekšskats. B, LDM 260/1, ārskats. **C**, pieaugušam īpatnim *Asterolepis ornata*, UP 10/1-1, ārskats. **D**, bruņuzivij *Pterichthyodes milleri*, ārskats (Hemmings, 1978, fig. 17 A).

**4.30. att.** Krūšu peldspuras brunu plātnes bruņuzivij *Asterolepis ornata* ar zobiņveida sutūru savienojumiem: mazuļiem (**A-D**), pieaugušiem īpatņiem (**E, F**). **A, B**, krūšu spuras pirmais centrālais vēdera kauls ($Cv_1$), iekšskats. LDM 260/152b. **C, D**, krūšu spuras otrais sānu vidējais kauls ($Mm_2$), iekšskats. LDM 260/152a. **E, F**, krūšu spuras trešais sānu malas kauls ($Ml_3$), ārskats. UP 10/1-6.

**4.31. att. A-C.** Krūšu peldspura bruņuzivs *Asterolepis ornata* mazulim. A, B, LDM 260/301a, ārskats. C, LDM 260/222b, iekšskats. **D, E**. Krūšu peldspuras distālais segments *Asterolepis ornata* pieaugušam īpatnim. D, pēc Gross (1931, Pl. VI, Fig. 3). E, UP 10/1-2. Lodes karjers. **F**, Krūšu peldspura bruņuzivij *Pterichthyodes milleri,* vidusdevons, Skotija (Hemmings, 1978, fig. 18 A).

**4.32. att.** Sutūrsavienojumu veidi starp galvas vairoga bruņu plātnēm bruņuzivij *Asterolepis ornata*. **A-E**, Zobiņveida savienojumu veids mazuļiem, ārskats. A, B, atdalījušās galvas bruņu plātnes LDM 260/5. C, atdalījušās galvas bruņu plātnes LDM 260/193. D, E, pakauša kauls LDM 260/250. **F, G**, Slīpais zobiņveida savienojumu veids pieaugušam īpatnim. Pineālais kauls, iekšskats, saglabājusies daži zobiņi. LDM 43/538.

**4.33. att.** Sutūrsavienojumu veidi starp bruņu plātnēm bruņuzivij *Asterolepis ornata*. Zaļās līnijas ir zāģveida savienojumi (krūšu peldspurām un daļēji galvas vairogam), sarkanās līnijas – zvīņveida savienojumi (pārklājumi) (rumpja muguras un vēdera sienām). **A,** pieaudzis īpatnis (pēc Lyarskaya, 1981, Fig. 74, ar nelielām izmaiņām pusmēness kaula reģionā). **B**, mazulis (Upeniece, Upenieks, 1992, Figs. 2B, 3B, ar nelielām izmaiņām pusmēness kaula reģionā).

**4.34. att.** Zvīņveida (pārklājumu) sutūrsavienojumu veids pieaugušām brunuzivīm *Asterolepis ornata*. A, priekšējā vidējā muguras plātne (AMD) UP 10/1-3, iekšskats. B, pakaļējā vēdera-sānu plātne (PVL), iekšskats (Lyarskaya, 1981, fig. 87-1). C, vidējā ventrālā plātne (MV), ārskats (Lyarskaya, 1981, fig. 88).

**4.35. att.** Bruņuzivs *Asterolepis ornata* mazuļa ar zvīņām klātā astes daļa. **A,** ar saglabājušos dorsālo peldspuru. LDM 260/80a, iekšskats (zvīņas ar tuberkulām ir ārskatā) (Upeniece, Upenieks, 1992, Pl.4, fig. 4). **B,** LDM 260/235a, iekšskats. Rāmītī fulkrālās zvīņas. **C,** LDM 260/88a, iekšskats. Rāmītī sānu zvīņas. **D, E,** LDM 260/9. **E,** nezināms simetrisks elements.

**4.36. att.** Dažu bruņuzivju (**A-E,H-J**) un telodontu (**F-G**) zvīņas. **A**, *Stensioella heintzi*, sānu zvīņa ārskatā. Apakšdevons, Vācija (Gross, 1962, fig. 6 B,G). **B**, *Pterichthyodes milleri*, sānu zvīņas ārskatā. Vidējais devons, Skotija (Hemmings, 1978, Fig. 22 C). **C**, Yunnanolepididae, sānu zvīņa ārskatā. Apakšdevons, Ķīna (Wang, 1991, fragment of Pl. 1 A). **D,E,H-J, *Asterolepis ornata,*** augšdevons, Latvija, Lodes karjers. **D, H-J, mazuļa astes zvīņas**, **D,** sānu zvīņas, ārskats un iekšskats (Ivanov et al., 1996, Fig. 8 I, M). **H-I,** kores zvīņas, iekšskats. **H**, pēc Upeniece, Upenieks, 1992, fig.4. **I**, LDM 260/9. **J**, sānu zvīņas, iekšskats (Ivanov et al., 1996, Fig. 8 L). **E**, **pieaugušas bruņuzivs zvīņa**, UP 10/1-5. **F,G,** telodonta *Gampsolepis insueta* zvīņas. Apakšdevons, Ukraina. **F**, ārskatā (Karatajūte-Talimaa, 1978, Pl. 48, fig.13) **G**, zvīņas plānslīpējums (ibid.: fig. 33-2).

**4.37. att.** Astes daļa ar dorsālo peldspuru sīka izmēra Yunnanolepididae bruņuzivij *Parayunnanolepis xitunensis*. Apakšdevons, Ķīna, Yunnan province. Paraugs V11679.1 (holotips), Mugurkaulnieku paleontoloģijas un paleoantropoloģijas institūts Pekinā, Ķīna.

**4.38. att.** Dermālo kaulu ornamentējuma attīstības secība brunuzivju *Asterolepis ornata* mazuļiem agrīnajās attīstības stadijās. **A**, Smalkā tīklojuma sākotnējā attīstība gar valnīšu sistēmas valnīšiem. Pirmā ontoģenētiskās attīstības stadija. PVL plātne LDM 260/500. **B**, Smalka tīklojuma ornamentējums klāj lielāko plātnes daļu. Starpstadija starp pirmo un otro ontoģenētiskās attīstības stadiju. AVL plātne LDM 260/577. **C**, **D**, Smalka tīklojuma ornamentējums. Otrā ontoģenētiskās attīstības stadija. C, AVL plātne LDM 260/489. D, ADL plātne LDM 260/472. **E**, Starpstadija starp otro un trešo ontoģenētiskās attīstības stadiju: smalka tīklojuma ornamentējums pārveidojas šūnveida ornamentējumā. AMD plātne LDM 260/357. **F**, Šūnveida ornamentējums. Trešā ontoģenētiskās attīstības stadija. PVL plātne LDM 260/521. Mēroga skala 1 mm.

**4.39. att.** Dermālo kaulu ornamentējums lielākiem *Asterolepis ornata* bruņuzivju mazuļiem. **A**, Šūnveida ornamentējums ar radiāli savienotiem valnīšiem. Ceturtā ontoģenētiskās attīstības stadija. AMD plātne, LDM 260/539. **B**, Tuberkulārais ornamentējums ar radiāli izvietotām tuberkulām valnīšu krustpunktos. Piektā ontoģenētiskās attīstības stadija. AMD plātne, LDM 260/78. **C**, Vienlaicīgi esoši trīs ornamentējuma tipi uz bruņu plātnes: 1, smalks tīklojums, 2, šūnveida, 3, tuberkulārs. AMD plātne, LDM 260/359. Mēroga skala 1 mm.

**4.40. att.** Dermālo kaulu tuberkulārs ornamentējums pusaugu (**A**) un pieaugušam (**B**) bruņuzivju *Asterolepis ornata* īpatnim. Mēroga skala 1 mm.

**4.41. att.** Bruņuzivju *Asterolepis ornata* mazuļi ar saglabājušos fosilizētu kuņģa saturu (St); ventrālais skats (dažas muguras bruņu plātnes ir ārskatā). **A,** LDM 260/260. **B,** LDM 260/1.

**4.42. att.** Bruņuzivs *Pterichthyodes milleri* neliela īpatņa rumpja bruņas; ventrālā sienas iekšskats ar detaļām (B,C) no dorsālās sienas, ārskats. Vidusdevons, Skotija. **A**, paraugs P4249 (Zviedrijas Dabas vēstures muzejā Stokholmā). **B**, fosilizēts kuņģa saturs (zem kreisās ADL plātnes). **C**, šūnveida ornamentējums uz PMD plātnes.

**4.43. att.** Paši mazākie atrastie bruņuzivju *Asterolepis ornata* mazuļi. Pirmais agrīnais dermālo bruņu plātņu attīstības posms (pirmā ontoģenētiskās attīstības stadija). A, Mazulis ar atdalītām bruņu plātnēm, LDM 260/200. B, Muguras bruņu plātnes ar atdalītu AVL plātni no ventrālās sienas, LDM 260/156. Augšdevons, Liepas (Lodes) mālu karjers, Latvija.

**4.44. att.** Bruņuzivju *Asterolepis ornata* mazuļi ar labi saglabājušos astes zvīņojumu. Otrais agrīnais dermālo bruņu plātņu attīstības posms (otrā ontoģenētiskās attīstības stadija). A, LDM 260/235b, dorsālais skats (Upeniece, 2001, Pl. 1, fig. 7). B, LDM 260/2, ventrālais skats.

**4.45. att.** Bruņuzivju *Asterolepis ornata* mazuļi. Trešais agrīnais dermālo bruņu plātņu attīstības posms (trešā ontoģenētiskās attīstības stadija), ventrālais skats. A, LDM 260/118a (Upeniece, 2001, Pl. 1, fig. 6). B, LDM 260/25.

**4.46. att.** Bruņuzivs *Asterolepis ornata* mazulis. Galvas vairoga bruņu plātnes un muguras priekšējā daļa. Ceturtais agrīnais dermālo bruņu plātņu attīstības posms (ceturtā ontoģenētiskās attīstības stadija). LDM 260/78.

**4.47. att.** Nepilnīgi saglabājies bruņuzivs *Asterolepis ornata* mazulis, dermālo bruņu plātņu piektā ontoģenētiskās attīstības stadija. Muguras puse. LDM 260/10.

**5.1. att.** Veseli akantožu (domājams, pieaugušu indivīdu) skeleti *Lodeacanthus gaujicus* Upeniece. **A**, LDM 270/19a; **B**, LDM 270/9a; **C**, LDM 270/7a.

**5.2. att.** Mazākais zināmais akantodes *Lodeacanthus gaujicus* mazuļa skelets bez zvīņojuma seguma (arī mazākā līdz šim aprakstītā akantode paleontoloģiskajā hronikā). Tās ķermeni vietām klāj saglabājusies ķermeņa krāsviela, galvu iezīmē tikai acu krāsviela un nedaudzie branhiostegālie stari. Par akantodes esamību liecina labi attīstītie peldspuru dzelkšņi un lāpstiņu kauli. **A**, LDM 270/45 a; **B**, zīmējums pēc abām parauga pusītēm: LDM 270/45 a, LDM 270/45 b.

**5.3. att.** Mezakantīda *Lodeacanthus gaujicus* rekonstrukcija (Upeniece, 1996, Fig. 4, ar nelielām izmaiņām) un mērītie attālumi: **as-caudal cleft**, attālums no anālās peldspuras dzelkšņa līdz *caudal cleft*; **as-ds**, attālums starp anālo un dorsālo peldspuru dzelkšņiem; **diam**, cirkumorbitālā gredzena ārējais diametrs; **ds-caudal cleft**, attālums no dorsālās peldspuras dzelkšņa līdz *caudal cleft*; **ps-as**, attālums starp krūšu un anālo peldspuru dzelkšņiem; **ps-ds**, attālums starp krūšu un dorsālo peldspuru dzelkšņiem; **ps-posterior end**, attālums no krūšu peldspuras dzelkšņa līdz astes galiņam; **ps-is**, attālums starp krūšu un starpspuru peldspuru dzelkšņiem; **ps-pls**, attālums starp krūšu un iegurņa peldspuru dzelkšņiem; **Y** – zvīņu skaits vienā milimetrā (dorsāli-prekaudālā reģionā).

**5.4. att.** Vislabāk saglabājušos akantožu *Lodeacanthus gaujicus* ķermeņa proporciju un zvīņojuma attīstības (dzeltenās joslas) shematisks attēlojums (Upeniece, 1996, Fig.3, ar izmaiņām). Sarkanās joslas norāda uz ķermeņa daļām, kuras ir segtas tikai ar ķermeņa membrānu, un uz tām vēl nav attīstījies zvīņojums (virs melnās horizontālās līnijas –

muguras pusē; zem – vēdera pusē). Vertikālā pārtrauktā līnija nodala visus skeletus pirmspektorālajā reģionā (galva + žaunas) un rumpī. Paraugu numuri kreisajā pusē. Skaitļi iekavās nozīmē teorētiskos ķermeņu garumus. Aptuveni mērījumi atzīmēti ar zvaigznītēm. Mērījumi milimetros.

**5.5. att.** Akantodes *Lodeacanthus gaujicus* nazālie kauli (Upeniece, 1996, Fig. 1 E, F, G). **A, B**, ar aptverošām tesērām, paraugs LDM 270/40a; **C**, nazālo kaulu pāris, LDM 270/34b; **D**, atsevišķs nazālais kauls, LDM 270/7a.

**5.6. att.** Akantodes *Lodeacanthus gaujicus* mazulis (Upeniece, 1996, Fig. 2 A, Pl. 1, Fig. 3) LDM 270/12 (kopgarums 23.0 mm). Zvīņojums sasniedzis endokrānija reģionu (en), zvīņojuma segums 84% (skatīt 5.4. att.). Zīmējums pēc abām parauga pusēm (LDM 270/12a; LDM 270/12b).

**5.7. att.** **A**, Akantodes *Lodeacanthus gaujicus* cirkumorbitālie (acu) kauli (Upeniece, 1996, Fig. 1H) in visceral view, pēc abām parauga pusītēm (LDM 270/2a; LDM 270/2b). Biezās līnijas = kaulu dabīgās robežas, plānās līnijas – kaulu redzamās robežas. Domājams, ka ir saglabājušies seši acu kauli. **B**, galva no tā paša parauga, LDM 270/2b. Sarkanīgie plankumi, iespējams, ir smadzeņu kapsulas atlieku fragmenti.

**5.8. att.** Akantodes *Lodeacanthus gaujicus* žokļu kauli (Upeniece, 1996, Fig.1 B-D). **A,B**, augšžokļi (aukslēju-kvadrāta kauli), paraugi LDM 270/29 un LDM 270/30; **C**, apakšžoklis (Mekeļa skrimslis), LDM 270/40.

**5.9. att.** Lāpstiņas kaula un krūšu peldspuras dzelkšņa artikulācijas reģions akantodei *Lodeacantus gaujicus* (Upeniece, 1996, Fig. 1 J). Paraugs LDM 270/18 a.

**5.10. att.** Piecu žaunu loku fragmenti akantodei *Lodeacanthus gaujicus*, sānskats, kreisā puse. Jautājuma zīme norāda uz nezināmiem elementiem. Paraugs LDM 270/14. **A**, fotogrāfija; **B**, zīmējums pēc tā paša parauga (Upeniece, 1996, Fig. 1 I).

**5.11. att.** Nepilnīgi saglabājušos akantožu *Lodeacanthus gaujicus* kaudālās daļas proporciju shematisks attēlojums (Upeniece, 1996, daļa no Fig. 3). A, LDM 270/11. B, LDM 270/13. C, LDM 270/10.

**5.12. att.** Akantodes *Lodeacanthus gaujicus* kaudālās peldspuras (Upeniece, 1996, Fig. 2 C, D, ar izmaiņām). **A**, domājams, pusaudža - pieauguša īpatņa starpstadija, LDM 270/11; **B**, domājams, pieaudzis īpatnis, LDM 270/13.

**5.13. att.** Akantodes *Lodeacanthus gaujicus* zvīņas un tesēras (Upeniece, Beznosov, 2002, Fig. 1; Pl.1, figs.1-7; Pl. 2). Sarkanie aplīši ir to precīzas atrašanās vietas. **A,B**, tesēras, paraugs LDM 270/34c-1A; **C-E**, zvīņas un to plānslīpejumi no rumpja zonas, LDM 270/15a-2B; **F-H**, zvīņas no aksiālās daivas, LDM 270/59-1c; **I,J**, zvīņas no rumpja zonas, LDM 270/55-1e; **K**, zvīņas plānslīpējums no rumpja zonas, LDM 270/15a1B. Mēroga skala 0.1 mm.

**5.14. att.** Akantodes *Lodeacanthus gaujicus* zvīņojums (Upeniece, Beznosov, 2002, Pl.1, Figs. 8,9) zvīņojums rumpja zonā. **A,B**, paraugs LDM 270/20. Mēroga skala 0.1 mm.

**5.15. att.** Akantodes *Lodeacanthus gaujicus* zvīņojuma zonas(Upeniece, Beznosov, 2002, Figs. 1, 2, ar izmaiņām). **1**, galvas dorsālā virsma; **2**, vaigu reģions; zvīņas no LDM 270/9a, LDM 270/38a; **3**, rumpja zvīņas; LDM 270/9, LDM 270/39; **4**, ventrālās zvīņas; LDM 270/9, LDM 270/7a; **5**, krūšu peldspuras zvīņas; **6**, astes peldspura: **6 a**, aksiālās daivas zvīņas; LDM 270/9; **6 b**, hipohordālās daivas zvīņas.

**5.16. att.** Divu tipu zvīņu pamatnes akantodes mazulī *Lodeacantus gaujicus*. Paraugs LDM 270/12. **A, B**, vesels skelets, abas parauga pusītes; **C-E**, zvīņojuma palielinājumi; **C**, zvīņu koniskās pamatnes no laterālās zonas (domājams, pilnībā attīstītas zvīnas); **D**, nepilnīgi attīstītas zvīņu pamatnes ar dziļu ventrālu iedobumu, vēdera zona; **E**, prepektorālā rajona zvīņas no muguras-sānu reģiona.

**5.17. att.** Zvīņas uz akantodes *Lodeacantus gaujicus* galvas laterālā reģiona (sk. 2.zonu 5.15.att.). Paraugs LDM 270/38a.

**5.18. att.** Ar zvīņojumu nepilnīgi segtas akantodes *Lodeacanthus gaujicus* galva LDM 270/46. Ir saglabājusies infraorbitālā sensorā līnija (infr). **A**, LDM 270/46b; **B**, kombinēts zīmējums pēc abām parauga pusītēm LDM 270/46a, LDM 270/46b.

**5.19. att.** Akantodes *Lodeacantus gaujicus* zvīņu plānslīpējumi (Upeniece, Beznosov, 2002, Plate 2). **A**, zvīņas kronas horizontālais plānslīpējums, LDM 270/15a-2B; **B**, zvīņas vertikālais plānslīpējums, LDM 270/15a-1B.

**5.20. att.** Akantodes *Lodeacanthus gaujicus* mazulis LDM 270/28. Zvīņojums attīstījies līdz dorsālās peldspuras dzelksnim (ds). Ķermeņa vidusdaļā ir saglabājušās ādas pigmentējuma atliekas (Upeniece, 1996, Fig. 2 B). 16 – zvīņu skaits vienā milimetrā. **A**, foto. **B**, zīmējums pēc tā paša parauga.

**5.21. att.** Akantožu *Lodeacanthus gaujicus* mazuļi ar nepilnīgi attīstītu zvīņojumu. Zvīņojums stiepjas diagonāli uz priekšu līdz iegurņa peldspuru dzelkšņu līmenim. Pārējo ķermeņa daļu iekontūrē saglabājies ķermeņa ādas pigmentējums. A, paraugs LDM 270/1 b; B, LDM 270/44 a.

**5.22. att.** Akantodes *Lodeacanthus gaujicus*, domājams, pieaudzis īpatnis (Upeniece, 1996, Fig. 1 A), skatīt arī zvīņojuma attīstības pakāpi 5.4. att. Holotips LDM 270/38. **A**, LDM 270/38a; **B**, zīmējums pēc abām parauga pusītēm: LDM 270/38a un LDM 270/38b.

**5.23. att.** Zvīņojuma un galvas elementu attīstības secība akantodei *Lodeacanthus gaujicus* **A**, bez zvīņojuma seguma; **B-D**, nepilnīgi attīstījies zvīņojums; **E**, pilnīgi attīstīts zvīņojums.

**5.24. att.** Zvīņojuma attīstības salīdzinājums Mesacanthidae **(A)** un Acanthodidae **(B-D)** dzimtām: **A**, *Lodeacanthus gaujicus* Upeniece (Upeniece, 2011); **B**, *Acanthodes gracilis* Beyrich (Zajic, 2005, Fig. 23); **C**, *Acanthodes bridgei* Zidek (Zidek, 1976, Fig. 13); **D**, *Acanthodes bronni* Agassiz (Heidtke, 1990, Fig. 52).

**5.25. att.** Proporciju izmaiņas starp prepektorālo garumu un ķermeņa kopgarumu augšanas laikā.

**5.26. att.** Peldspuru dzelkšņu proporciju izmaiņas augšanas laikā. **A**, starp starpspuru (is) un anālās peldspuras (as) dzelkšņiem; **B**, starp starpspuru (is) un krūšu peldspuras (ps) dzelkšņiem; **C**, starp iegurņa (pls) un krūšu peldspuras (ps) dzelkšņiem; **D**, starp iegurņa (pls) un anālās peldspuras (as) dzelkšņiem.

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