ACADEMIA

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FOSSIL FISHES AS LIVING ANIMALS

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FOSSIL FISHES AS LIVING ANIMALS

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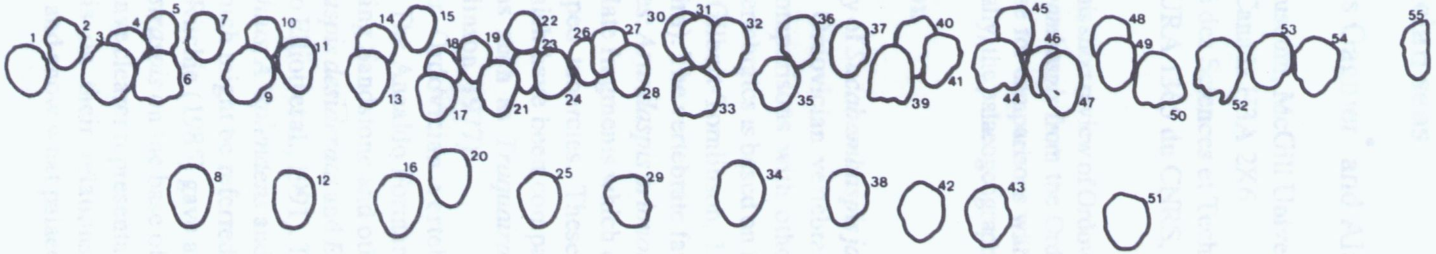
Preface

In 1989, the Second International Colloquium on the Middle Palaeozoic Fishes was held in Tallinn. The aim of the Colloquium was to activate the studies in fossil fish ecology, functional morphology and other palaeobiological fields of knowledge. That is why the title of the book, previously the motto of the meeting (proposed by Dr. Daniel Goujet, Paris) is "Fossil Fishes As Living Animals". The volume includes a significant part of the papers and posters presented at the Colloquium.

The papers of the volume deal with the fossil fishes of a wide age interval, mostly from the Ordovician to the Permian, but more recent forms are not excluded either. From the point of view of systematics, all major groups of the early vertebrates - thelodonts, heterostracans, osteostracans, placoderms, chondrichthyans, acanthodians, crossopterygians, dipnoans and actinopterygians are considered. The topics include ecology of both fossil agnathans and fishes, functional morphology, in particular locomotion and feeding mechanism, and fish assemblages in various environments, analyzed from somewhat different viewpoints. Also biomineralization, an almost new subject in fossil fish studies, ontogeny and growth of skeletal elements in the representatives of several groups (e.g. heterostracans, chondrichthyans and dipnoans) and relationships between different groups, taphonomy of fishes and associated invertebrates as well as palaeobiogeography have been discussed. A number of unique finds, e.g. juveniles of antiarchs, cranial material of the Early Devonian palaeoniscoids, articulated acanthodians of the same age, and new forms coming from the regions poorly known from the aspect of fossil fishes (e.g. Kirgizia, Nevada) are described. Taking into account the variety of subjects considered in the papers, their arrangement in groups is somewhat provisional.

The volume could have hardly been prepared for print without the linguistic help of Mrs. Anne Noor and Mrs. Irene Tiivel, an assistance with illustrations of Mrs. Kaie Ronk, and active cooperation of Dr. Madis Rubel, and Ivar Puura, Institute of Geology, Tallinn. To them the editor should like to express her sincerest thanks.

The 2nd International Colloquium on the Middle Palaeozoic Fishes, the sixth in a series of international meetings on Palaeozoic fishes, aroused wide interest. Colleagues from 15 countries (Australia, Canada, China, Estonia, France, Germany, Holland, Latvia, Lithuania, Norway, Poland, Sweden, UK, USA, and USSR) participated in the Tallinn meeting in September, 1989, and in the following excursions to the Silurian fish-localities on Saaremaa Island (West of Estonia) and the Devonian localities in South Estonia and North Latvia. Exhibitions of fossil fishes and possibilities to study rich collections were presented at the Institute of Geology, Acad. Sci. Estonia, Tallinn and in Nature Museum of Latvia, Riga.



A photo (by E. Grünberg) taken in the Town Hall Square shows participants and organizers. From left to right are: 1. Wang Nian-Zhong, 2. J. Nõlvak, 3. S.V.T. Young, 4. J. Valiukevičius, 5. P. Männik, 6. R. Mertiniene, 7. M.D. Gottfried, 8. P.E. Ahlberg, 9. V. Karatajūte-Talimaa, 10. A.A. Bray, 11. Pan Jiang, 12. D. Goujet, 13. L. Lyarskaya, 14. H.-P. Schultze, 15. U.J. Borgen, 16. R.R. Ilyes, 17. O. Obrucheva, 18. D. Fredholm, 19. T. Meidla, 20. V. Kuršs, 21. N. Krupina, 22. A. Blieck, 23. T. Safonova, 24. L. Novitskaya, 25. J. Upenieks, 26. D. Esin, 27. M. Belles-Isles, 28. S. Malinovskaya, 29. M. Ginter, 30. M. Otto, 31. A. Ivanov, 32. M. Minich, 33. I. Upeniece, 34. O. Lebedev, 35. L. V'yushkova, 36. J.W. Reed, 37. J. Vergoossen, 38. E. Lukševičs, 39. K. Dennis-Bryan, 40. A. Kuznetsov, 41. E. Mark-Kurik, 42. N. Panteleyev, 43. V. Voichishin, 44. H. Lelièvre, 45. D. Vézina, 46. A. Kleesment, 47. M.M. Smith, 48. P.-Y. Gagnier, 49. Liu Yuhai, 50. S. Turner, 51. P. Chekhovich, 52. L. Nikolaichuk, 53. D. Pavlov, 54. A. Zhivkovich, 55. J.A. McAllister;
1,11,49 - Beijing, 2,5,19,41,46 - Tallinn, 3,39,47 - London, 4,6,9 - Vilnius, 7,14,55 - Kansas, 8 - Cambridge, 10 - Reading, 12,44,48 - Paris, 13,20,25,33,38 - Riga, 15 - Stockholm, 16 - Oslo, 17,21,24,26,28,34,40,42,51,54 - Moscow, 22 - Villeneuve, 23,32 - Saratov, 27 - Tübingen, 29 - Warszawa, 30 - Marburg, 31,53 - St. Petersburg, 35 - Novosibirsk, 36 - Portland, 37 - Groningen, 43 - Lvov, 45 - Miguasha, 50 - Brisbane, 52 - Kiev (later changes of whereabouts not indicated). Absent or unfortunately invisible in the photo are: O. Afanassieva, G. Zakharenko (Moscow), R. Cloutier (Kansas), T. Märss, A. Noor (Tallinn), E. Pihu (Tartu) and R. Sorkina (St. Petersburg).

On *Sacabambaspis janvieri* and the vertebrate diversity in Ordovician seas

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Abstract. In this short review of Ordovician vertebrates, the authors summarize preliminary data on *Sacabambaspis* from the Ordovician of Bolivia (age, taphonomy, morphology). This is the base for comparisons with the Ordovician vertebrates of North America and Australia. Finally, the palaeogeographical problem of this distribution is settled.

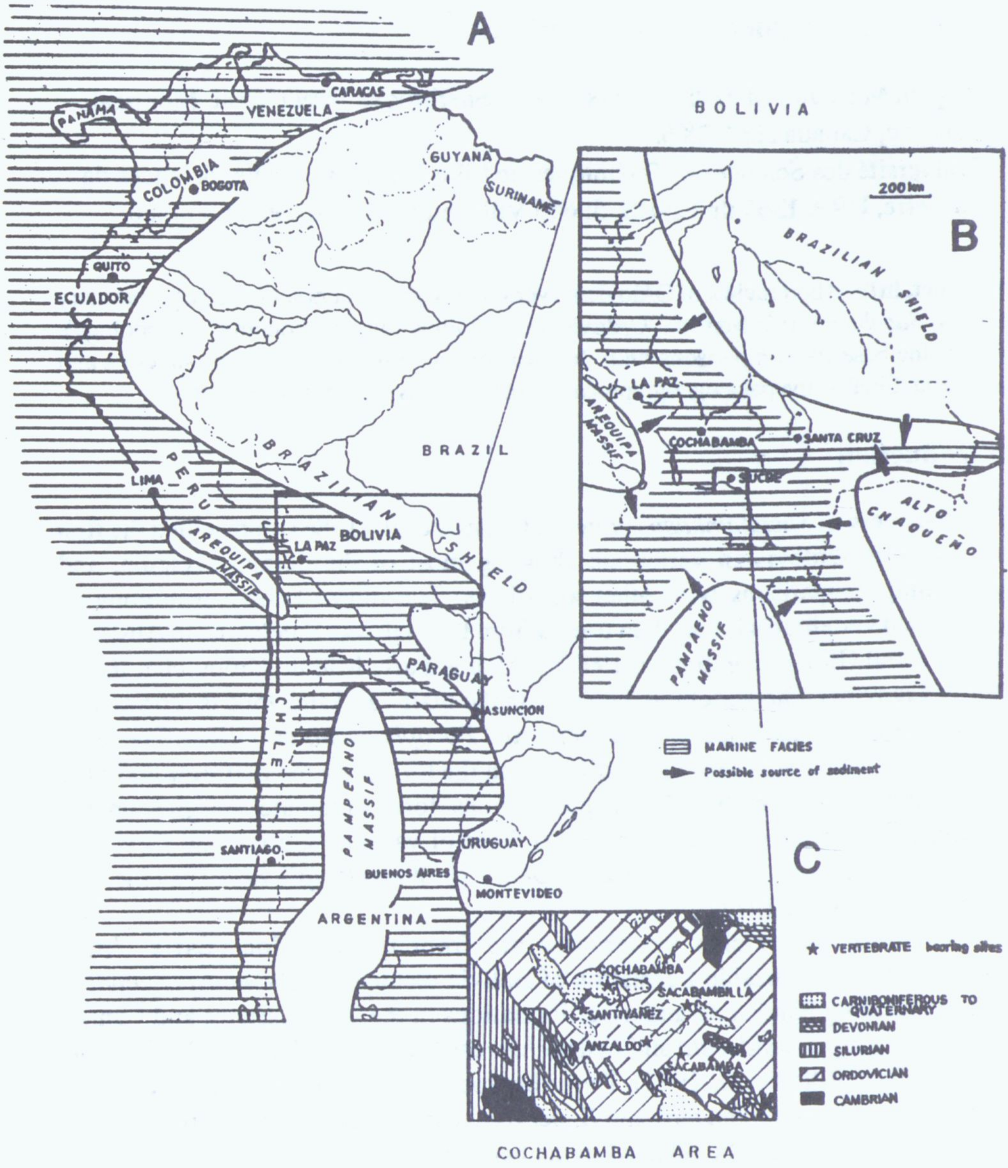
Introduction

The discovery of *Sacabambaspis janvieri* Gagnier et al. (1986) represented the first record of an Ordovician vertebrate showing most of the dermal skeleton, and permitting comparisons with other agnathans. The oldest known testimony of undisputed vertebrates is based on fossils from the Stairway Sandstone in Australia (Ritchie and Gilbert-Tomlinson, 1977), which is Early Middle Ordovician in age (Early Llanvirn). The vertebrate fauna from the Stairway Sandstone is represented by two species: *Arandaspis prionotolepis* and *Porophoraspis crenulata*. The latter is based on plate fragments which differ from the former by the perforations in the diamond-shaped tubercles. These perforations form crenulate margins on the tubercles, which have been compared to those of various Silurian and Devonian heterostracans such as *Traquairaspis plana* or *Weigeltaspis alta* (Ritchie and Gilbert-Tomlinson, 1977).

The other Ordovician vertebrates are from the Caradoc (Early Upper Ordovician). The Anzaldo Formation of Bolivia yielded *Sacabambaspis janvieri*, and the Harding Sandstone and other formations in the United States and Canada gave up *Astraspis desiderata* and *Eriptychius americanus* Walcott (1892; for more details refer to Elliott et al., 1991). Two other species have been referred to *Astraspis* and *Eripthychius*, *A. splendens* and *E. oervigi*, respectively, but these are based on fragments which might be referred to the two former species.

Recently Ritchie (1985) gave a redescription of *Arandaspis* and Elliott (1987) reassessed *Astraspis* on the base of new specimens.

We now have clearer representation of most of the Ordovician forms, permitting an hypothesis on their relationships. So we intend here to highlight those relationships and show what palaeogeographic problems they lead to.

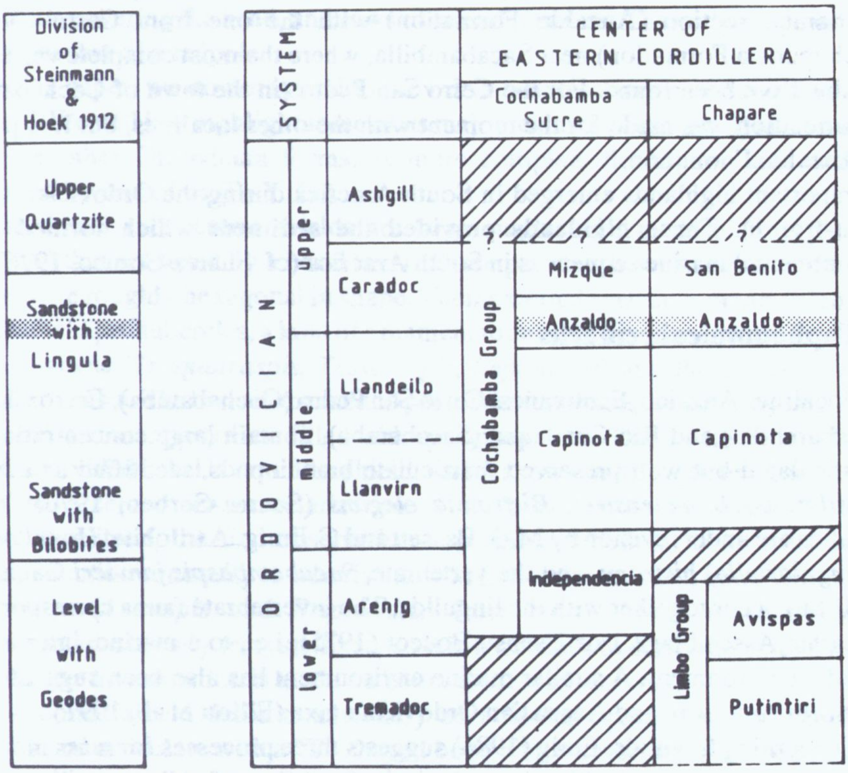


Text-fig. 1. Map of western South America showing the distribution of Ordovician rocks on a present geography (A). An interpretation of Ordovician highlands and seaways of Bolivia is given in (B) with arrows showing the possible sediment sources (after Suarez-Soruco, 1976). (C) is a simplified geological map of Cochabamba, based on the Mapa Geologico de Bolivia (GEOBOL) [Note that these schemes do not care of the tectonic structure of the Andes, nor their original Ordovician relationships].

I - On *Sacabambaspis janvieri*

A) Geological setting and age

The most complete sequence of Ordovician rocks in Bolivia occurs in the Eastern Cordillera (Text-fig. 1), which extends from the Peruvian border to Argentina. All the localities where Sacabambaspis was found (Text-fig. 1), occur in the Anzaldo Formation (the term of Cuchupunata Formation is used by some authors, but it represents the same unit: it is only a question of priority in the name) which could reach a thickness of 2000 metres. In the Cochabamba area, Steinmann and Hoek (1912) were the first to distinguish different Ordovician rocks, based principally on their associated fauna. They described three levels, viz. from the base to the top, "Bilobites Sandstein". "Lingula Sandstein" and "oberer Quarzit". Later the upper sandstone received the name of the San Benito Formation, and the two lower ones now form the Anzaldo Formation (Text-fig. 2).



Text-fig. 2. Simplified stratigraphical sequence of the Ordovician of the central Eastern Cordillera of Bolivia (modified from Rivas, 1971 in Suarez-Soruco, 1976). The location of the lingulid sites is indicated in grey.

The precise age of the Anzaldo Formation is debated: Suarez- Soruco (1976) considers it is Caradoc in age, but G. Rodrigo de Walker and M. Toro (pers. comm.) argue for a Llanvirn-Llandeilo age based on the generic reattribution of a trilobite encountered in this formation. Gagnier (1987) thought that the vertebrate from those localities is related to the forms from Australia which are of Early Llanvirn age (Ritchie and Gilbert-Tomlinson, 1977; Webby, 1981). There is no fossil known to date from this formation, but the Capinota Formation, below, is Llanvirn- Llandeilo in age (Suarez-Soruco, 1976) or Llanvirn (Aceñolaza and Baldis, 1987), on the base of the graptolite *Didymograptus murchisoni* and the trilobite *Hoekaspis matacencis*; and the San Benito Formation, above, is Caradoc after the bivalve *Ctenodonta cochabambensis*.

Sacabambaspis was first described from Sacabamba, from the basal part of the local section composed of 300 metres of lutites, well-bedded yellowish sandstones with limonite alteration and grey to greenish grey and yellow sandstones. A few metres below and above the vertebrate-bearing levels are phosphorite levels, principally composed of crushed lingulid shells, in which some small vertebrate fragments were found. Rodrigo de Walker and Toro (1987) correlated the Sacabamba section (Anzaldo Formation) with the one from Cerro Chakeri (Cuchupunata Formation) near Sacabambilla, where the most complete vertebrate remains have been found. For the Cerro San Pedro (in the town of Cochabamba) no correlation was made for the moment with the other localities, but it is part of the Anzaldo Formation.

Important highlands emerged in South America during the Ordovician epoch (Text-fig. 1). These highlands provided the sediment which formed thick epicontinental marine sequences in South America (cf. Suarez-Soruco, 1976).

B) Taphonomical remarks

The localities Anzaldo, Santivañez, Cerro San Pedro (Cochabamba), Cerro Chakeri (Sacabambilla) and Rio Challaque (Sacabamba), contain large concentrations of disarticulated but well preserved inarticulate brachiopods, identified as *Lingula ellipsiformis*, *L. muensteri*, *Bistramia elegans* (Suarez-Soruco, 1976). These lingulids are under revision by M.G. Bassett and C. Emig. A trilobite, *Homalonotus (Brongniartella) bistrami*, and the vertebrate, *Sacabambaspis janvieri* Gagnier et al. (1986) occur together with the lingulids. The invertebrate fauna corresponds to a Benthic Assemblage 1 or 2 sensu Boucot (1975), i.e., to a marine, intertidal or subtidal environment. A similar marine environment has also been suggested for the North American and Australian Ordovician taxa (Elliott et al., 1991).

Concerning lingulids, Emig (1986) suggests three processes for mass mortality outside their burrows: a sudden drop of salinity, an inflow of sediment with particles bigger than 0.5 mm, and/or the destruction of substratum by a storm. Since the sediment in the vertebrate-bearing level of Sacabambilla is fine-grained, Gagnier (1987) proposed that massive inflow of fresh water brought by a storm or a nearby river, may have produced the mortality of the lingulids and, to some extent, the vertebrates. However it does not explain entirely the fossilization process, which requires a massive input of sediment (Emig, pers. somm.). The quality of the articulated vertebrates is good. The Sacabambilla locality yielded about 30 articulated specimens, concentrated in a small area, many of them being packed side-by- side and some one-over-the-other.

C) General external structure of *Sacabambaspis janvieri*

Preliminary studies of *Sacabambaspis janvieri* were based on fragmentary material and the discovery of more complete specimens requires reinterpretation of some earlier observations. Gagnier et al. (1986) and Gagnier (1987) described some fragments thought to be ventral shields (e.g., the holotype MNHN BOL V-3282), but which are in fact from dorsal shields (Gagnier, 1989).

The average length of the animal is about 35 cm, of which the head shield represents more than a third. The shield is about 8 cm broad. The overall morphology is quite similar to that of *Arandaspis* from Australia, with two large bone units covering the head, and rows of lateral platelets. The body shape vaguely resembles that of a tadpole.

In this paper, we do not intend to provide a full description of *Sacabambaspis janvieri*. We will just highlight some of its major features (Text-fig. 3) and compare it to the other Ordovician forms. A more complete description will soon be published by one of us (P.-Y. G.).

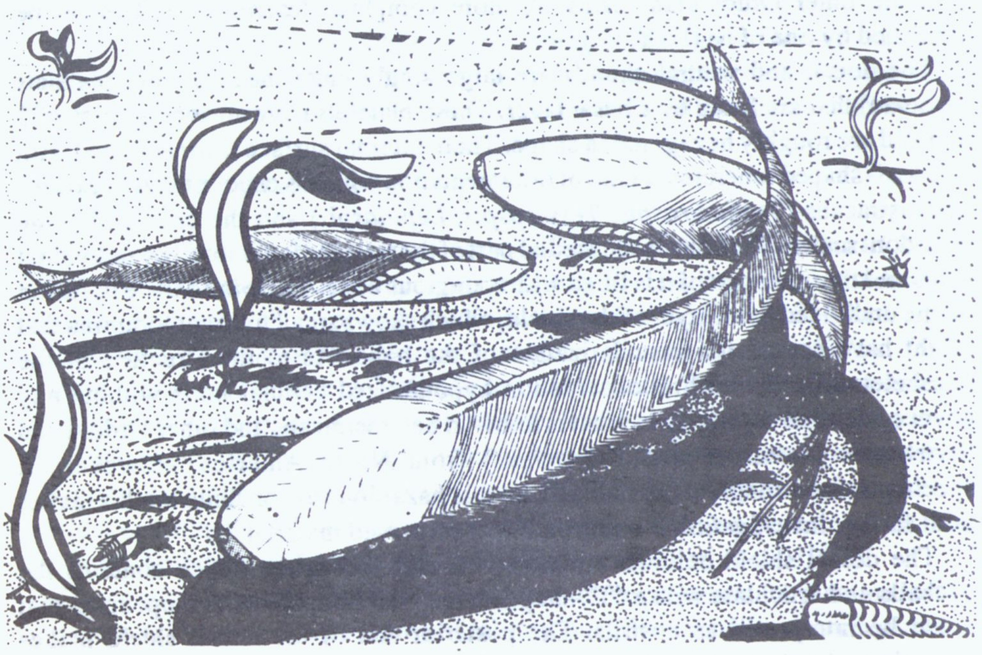
The dorsal and ventral shields are large single units made of tiny platelets (tesserae) that are fused by a basal layer. These platelets have an average size of 2 mm and are roughly hexagonal in shape. Their external surface is ornamented with oak-leaf- shaped tubercles, a kind of ornamentation which is encountered in various heterostracans (*Traquairaspis*, *Tesseraspis*, *Lepidaspis*) and the crown of some thelodont scales. The bone in the medial part of the tesserae is enclosed by individual walls and the inner part of it is filled with spongious bone. There is no trace of fusion on the undivided basal layer of the shield, which shows small nutrient foramina that might have served for vascularization of the bone. As to the structure of the exoskeleton itself, the first observation hypothesized cellular bone without any cover of dentine contrarily to what is know in heterostracans and other Ordovician vertebrates (*Astraspis* and *Eriptychius*) from North America. However all specimens are strongly recrystallized, so it is hazardous to conclude on this matter until further investigation is made on better preserved material.

The dorsal shield delimits anteriorly an elliptical space which contains the eyeballs and articulate with a "T"-shaped bone which separates two openings that could be interpreted as nostrils. The posterior end of the dorsal shield makes transition with the body scales. In this region there is a low median crest followed posteriorly by dorsal median ridge scales.

On the dorsal shield, there is a paired depression located 2.5 cm from the anterior median margin of the shield. Posterior to this paired depression, the tubercles of the tessellated units are smaller and their orientation gives a false impression that there is a separate plate. It is interpreted as a paired pineal- parapineal apparatus because of the modified ornamentation of the surrounding platelets (Gagnier, 1989).

The ventral shield is deep and convex. The anterior 2.5 cm are made up of square-shaped platelets aligned in rows to form the exoskeletal mouth apparatus. This may represent an arrangement of scales on the lip or a postoral field as in some cephalaspids (*Hirella*; Heintz, 1939). In ventral view, it is oval in shape. It is strongly convex anteriorly and becomes flattened posteriorly, so that in lateral view it appears higher anteriorly and slopes posteriorly, disappearing at the posterior end. Its posterior end is a median, rounded, convex lobe onto which body scales are attached and form a ventral median ridge.

On each side of the head, the dorsal and ventral shields are united by a series of marginal plates. These are diamond-shaped (lozangic), with a little posterior knob at mid height; they are about 20 in number and extend from approximately the level of the pineal openings to the posterior end of the ventral shield. They probably are covers for the branchial external openings.



Text-fig. 3. Artist's illustration of *Sacabambaspis janvieri* swimming in an Ordovician sea of Bolivia. The tail is extrapolated from three partially articulated specimens (from Gagnier, 1989; courtesy of Nation. Geogr. Res.). •

The remainder of the body is covered with rows of thin, elongated scales ornamented with oak-leave-shaped tubercles similar to those of the shields but arranged in parallel rows. There are four main scale rows covering the flank parts of the body, plus two small ones which form the dorsal and ventral median scale ridges. The four main rows are arranged two-by-two in "chevrons". There are more than a hundred scales along the chevrons axes. The scaled part of the body is about twenty five cm long, of which ten make the tail. The ventral median ridge scales seem to end before the tail, in the region interpreted as the cloacal opening. The tail seems to have a long "rat-tail-shaped" cordal extension.

The sensory-line system of the dorsal shield is represented by two anterolaterally curved grooves previously described in the holotype and on specimen YPFB PAL-6206 (Gagnier, 1987). These sensory grooves may possibly be supraorbital and infraorbital lines. There is also a discontinuous paired medial sensory groove (the medial dorsal line) which runs from the back to the shield near the paired pineal-parapineal depression; at this point it turns laterally. In front of the paired depression, there are two small pit-lines. On the ventral shield, the sensory-line pattern consists of a paired medial discontinuous line turning laterally near the mouth border, and forming the postoral line. In the lateral part of the shield there is another discontinuous groove which runs posteriorly from the oral region on the posterior two thirds of the shield and which turns ventromedially. A series of laterally placed transversal commissures (18 to 20 in number) are situated ventrally to each marginal plate. There is a pair of ventral lateral lines on the body scales which run from the ventral shield for two thirds of the length of the body. They are marked by a continuous and straight groove on the surface of the scales.

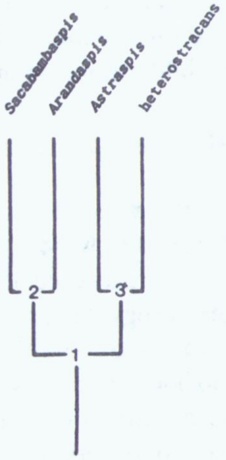
II - Ordovician vertebrates and their relationships

The first record of Ordovician vertebrates was from North America (*Astraspis* and *Eriptychius* Walcott, 1892). These taxa were identified as heterostracans on the basis of their histology, especially the presence of cancellous or spongy aspidin (an acellular bone) which is classically regarded as typical for the heterostracans. The Australian genus *Arandaspis* was also identified as heterostracan (Ritchie and Gilbert-Tomlinson, 1977) but no bone structure was preserved; this attribution was based on the presence of two large shields covering the head and the detail of the ornamentation resembling that of some heterostracans.

Sacabambaspis shares several features with heterostracans – large ventral and dorsal shields covering the head; a dermal shield structure which consists of polygonal units; ornamentation of oak-leaf-shaped tubercles; anterior position of two nostrils; preanal median ridge scales; a pineal sensory line; and (only in a few heterostracans) a grooved sensory-line. From these characters, only the covering of the head with at least two large shields may be regarded as a synapomorphy of *Sacabambaspis* and heterostracans. The polygonal structure of the dermal skeleton and the pineal lines are also encountered in osteostracans. The galeaspids show grooved sensory lines. The preanal median ridge scales are certainly a primitive condition for the craniates since they may correspond to the preanal ridge of myxinoids and cephalochordates, and are probably related to the absence of unpaired fins (cf. Janvier, 1981).

Comparison of the vertebrate from Sacabamba and Sacabambilla with those of the other Ordovician localities reveals the following similarities and differences. The sculptute of the shield ornamentation shows a gradation between *Arandaspis*, *Porophoraspis* and *Sacabambaspis*, starting from diamond-shaped-tubercles which would be sculptured into an oak- leaf tubercle (G. C. Young, pers. comm.). The elongated tubercles of *Eriptychius* seem closer to this pattern than the stellate ornamentation of *Astraspis*. *Sacabambaspis* shares with *Arandaspis* the branchial opening arranged in a slanting row, each one being covered by a platelet, whereas these seem to form a horizontal row in *Astraspis* (Elliott, 1987). The double pineal depression in *Sacabambaspis* and *Arandaspis* is not visible on *Astraspis*. The elongated shape of the body scales occurs also in *Eriptychius* (Sawin, 1959; Pl. II fig. 3), but is closer to that in the rhombic scales of *Astraspis* (Elliott, 1987). The eye ring of *Sacabambaspis* is not known in other Ordovician taxa.

The comparison of these three taxa shows that *Sacabambaspis* and *Arandaspis* are closer to each other than to the North American genus *Astraspis*, and thus can be united in the same group (Text-fig. 4).



Text-fig. 4. Hypothesis of phylogenetic relationships of Ordovician vertebrates.
1: Large plates covering the head, long and thin rod scales, strictly pelagic forms, development of oral plates.
2: Sensory line system born in surface grooves on the cephalic region and on the body scales; individual platelets on the branchial openings; pineal and parapineal apparatus.
3: Reduction of the number of branchial openings, development of dentine tissue (mesodentine) and the pineal-parapineal organs get arranged antero-posteriorly. Heterostracans and *Astraspis* are individualized by the presence of acellular bone and the dorsalisation of the branchial openings.

The anterior position of the olfactory capsules and possibly paired nostrils in the heterostracans, as argued by Novitskaya (1975), refutes the hypothesis of the presence of prenasal sinus (Stensiö, 1927, 1964, 1968; Janvier, 1975, 1981). This feature, shared with *Sacabambaspis*, would be closer to the gnathostome condition than to the nasohypophyseal or nasopharyngeal opening of lampreys and hagfishes. If this relation to gnathostomes is accepted, it would mean that muscularized fins in gnathostomes and osteostracans appeared twice in vertebrate history or, on the contrary, that the nasohypophyseal opening is primitive.

Among characters which differentiate *Sacabambaspis* and *Arandaspis* from the heterostracans, are the paired pineal- parapineal openings side-by-side. Bjerring (1975) could not find any embryological evidence to define this condition as primitive or apomorphic. The large number of branchial openings is a widespread character, and probably primitive among craniates. The presence of a single opening corresponds to an apomorphy for the heterostracans (sensu Lankester, 1868-70).

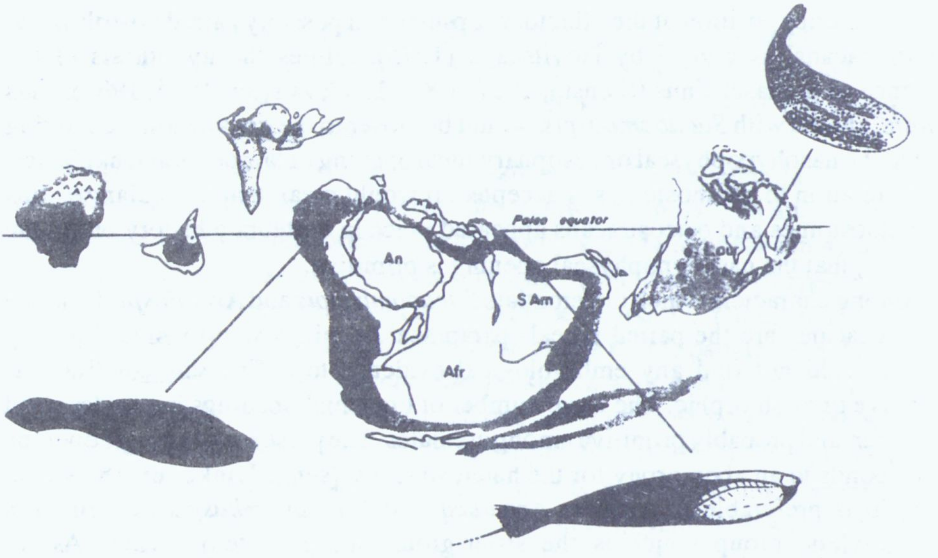
So it is preferable to consider *Arandaspis* and *Sacabambaspis* as forming a monophyletic group which is the sister-group of true heterostracans. As for *Astraspis* and heterostracans, a closer relationship seems probable (Text- fig.4).

III - Palaeogeographical interpretation

As shown in Text-fig. 5, Ordovician vertebrates have been collected in three distant geographical areas, viz., central Australia (Amadeus Basin), Bolivia (Cochabamba region) and North America (USA and Canada). On most recent palaeogeographical reconstructions (e.g., Scotese, 1986), the three records fall within the warm Ordovician zones, near the palaeoequator. All are derived from lingulid- and *Cruziana*-bearing sandy facies, interpreted as near-shore, intertidal to subtidal marine. The problem is then to know if the observed distribution may be easily explained on the palaeogeographical reconstruction (Text- fig. 5).

Arandaspis and *Sacabambaspis* have been collected from countries which are thought to have been parts of a single continental platform, at the edge of Gondwana, in Ordovician times (Text-fig. 5: Australia and South America). As both taxa are phylogenetically related (Text-fig. 4), it seems that no strong problem arises here. However, *Astraspis* and *Eriptychius* come from North America which is supposed to have been separated from Gondwana. In this case, if Ordovician vertebrates, such as heterostracans, were unable of transoceanic migrations (Blieck, 1985; Blieck and Janvier, 1991), we need a more compact reconstruction of the Pangeic type, with a closed paleo-Pacific ocean (Gagnier et al., 1986), to explain the occurrence of the North American taxa.

Using a vicariant analysis better than a migratory one, we also need a pre-Mid Ordovician compact reconstruction, with a generalized distribution for the ancestral species to all Ordovician vertebrates (Elliott et al., 1991). As it is not the case on any published reconstruction (e.g., Scotese et al. 1979; Scotese, 1986), we conclude that the observed distribution does not fit the palaeogeographic reconstructions.



Text-fig. 5. Palaeogeographic reconstruction (after Scotese, 1986) for the Ordovician (Llandeilo-Caradoc) with location of the Middle and Upper Ordovician vertebrate records. Shallow seas (grey) slightly modified after Turner (1978). The black triangle refers to the *Arandaspis-Porophoraspis* assemblage from Australia (Ritchie, 1985). The black circles refer to the *Astraspis-Eriptychius* assemblage from North America (reconstruction of *Astraspis* in right lateral view after Elliott, 1987). The black star refers to *Sacabambaspis* from Bolivia (Gagnier, 1989).
Abbreviations: AFR Africa, AN Antarctica, AU Australia, IC Indochina, IN India, KAZ Kazakhstan, LAUR Laurentia, SAM South America, SIB Siberia.

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Thelodont lifestyles

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Abstract. Thelodonts are extinct Palaeozoic agnathan fishes characterized by an exoskeleton of discrete dentinal scales with a base of bone-like tissue capable of growth. Isolated scales are known from a wide range of sedimentary lithologies including true bone beds from around the world, mostly preserved in open shelf marine environments. Less than a fifth of described species are known from articulated specimens from low-energy deposits in Scotland, Norway, Estonia, Britain and Canada. Such specimens give information about the form, life style and habitat of thelodont species. Some thelodonts, such as *Lanarkia*, were fusiform, apparently active nektonic forms; others, such as *Turinia*, were probably bottom-dwellers with a demersal lifestyle like modern rays and squatinid sharks.

Introduction

Thelodonts existed for about 80 million years from Late Ordovician to early Late Devonian times. Their scales are the commonest vertebrate remains in the Early Silurian and are common also in certain deposits into the Devonian. Their biostratigraphical usefulness as microfossils and their presence in marine, brackish and possibly non-marine sediments has led to a resurgence of interest in thelodonts in recent years.

Thelodont natural history appears veiled in mystery. Presumably, thelodonts were essentially soft-bodied, with a largely uncalcified cartilaginous skeleton; only the exoskeleton of almost indestructible dentinous scales is usually preserved. The scales are mostly found isolated. Less commonly they occur in undisturbed patches of squamation and sometimes as complete squamation cover.

Turner (in press) recently reviewed geographic and stratigraphic evidence bearing on the distribution of thelodonts. She concluded that nearly all thelodonts lived in marine environments, mostly in openshelf waters, associated with conodonts, brachiopod and other shelly faunas of B.A. 2-3 type. Some may have been able to withstand wide salinity changes. In the Silurian and Devonian, thelodont scales are found in limestones from shallow to deeper water environments. Few and complete specimens are preserved in sediments that are sometimes regarded as freshwater in origin; these include the higher Silurian fish beds of Scotland and Norway, and sites in the Early Devonian of the Welsh Borderland. Thelodonts also occur in sediments interpreted as from highly restricted, hyposaline lagoonal or brackish-water environments, including the nikoliviids of Arctic Canada, and thelodont scales in the Water Canyon Formation and equivalents of Utah and Colorado.

Whole specimens provide information on the overall morphology of thelodonts, along with some indications of the internal structures. A major problem since the first articulated thelodonts were found 120 years ago has been to ascertain the identity and functional significance of these structures.

Early restorations portrayed thelodonts as flattened animals with a heterocercal tail (Powrie, 1870; Traquair, 1899a,b, 1901, 1905). Recent reconstructions (e.g. Ritchie 1968a; Turner, 1970) show them more life-like and fusiform. Rarely are they portrayed as active swimmers; one such illustration is that of *Lanarkia* by Alice B. Woodward in Knipe (1912). This paper summarizes the evidence of thelodont morphology and provides a fresh picture of three species, *Lanarkia spinosa*, *Turinia pagei* and *Canonia*? *heintzae*. New restorations (Text-figs 1A-C) of these animals are based on diagrammatic sketches of actual specimens (Turner, 1984).

General morphology

Basic morphology is discussed by Ritchie (1963, 1968a-c), Märss (1979, 1982), Hout (1990), and Turner (1982, 1984, 1986, 1991, in press, in prep.). Here the salient points are discussed and presented in Table.

The Thelodonti are placed among the jawless fishes (agnathans). They appear to be simple fusiform or flattened animals, up to 1 m long, with an exoskeleton of dermal scales set in a complex squamation. Since the first discovery of thelodonts in the early 1800s, some 60 species in 16 genera have been described, mostly from isolated scales. Often, the arrangement and shape of the dermal scales are the only clues to underlying body structures.

The cephalothorax made up one quarter to one third of total length, with the tail sometimes reaching similar proportions. In dorsal or ventral view the anterior margin of the head was rather broad, with rounded anterolateral corners. When traced back from the eyes, the margins of the head gradually widen into elongate triangular lateral flaps. The mouth was terminal or nearly so. Evidence of paired nasal sacs exists in some species. The eyes, preserved as round bulges, holes in the squamation, or black carbonaceous stains, were placed well forward at the dorsolateral corners of the head. In *Phlebolepis elegans* there is a triangular rostral area dorsal to the mouth, covered with several transverse rows of rhomboid scales. Immediately behind this area is an indentation which Ritchie (1968a) interpreted as the possible site of the pineal organ. This structure has not been recognized in any other thelodont.

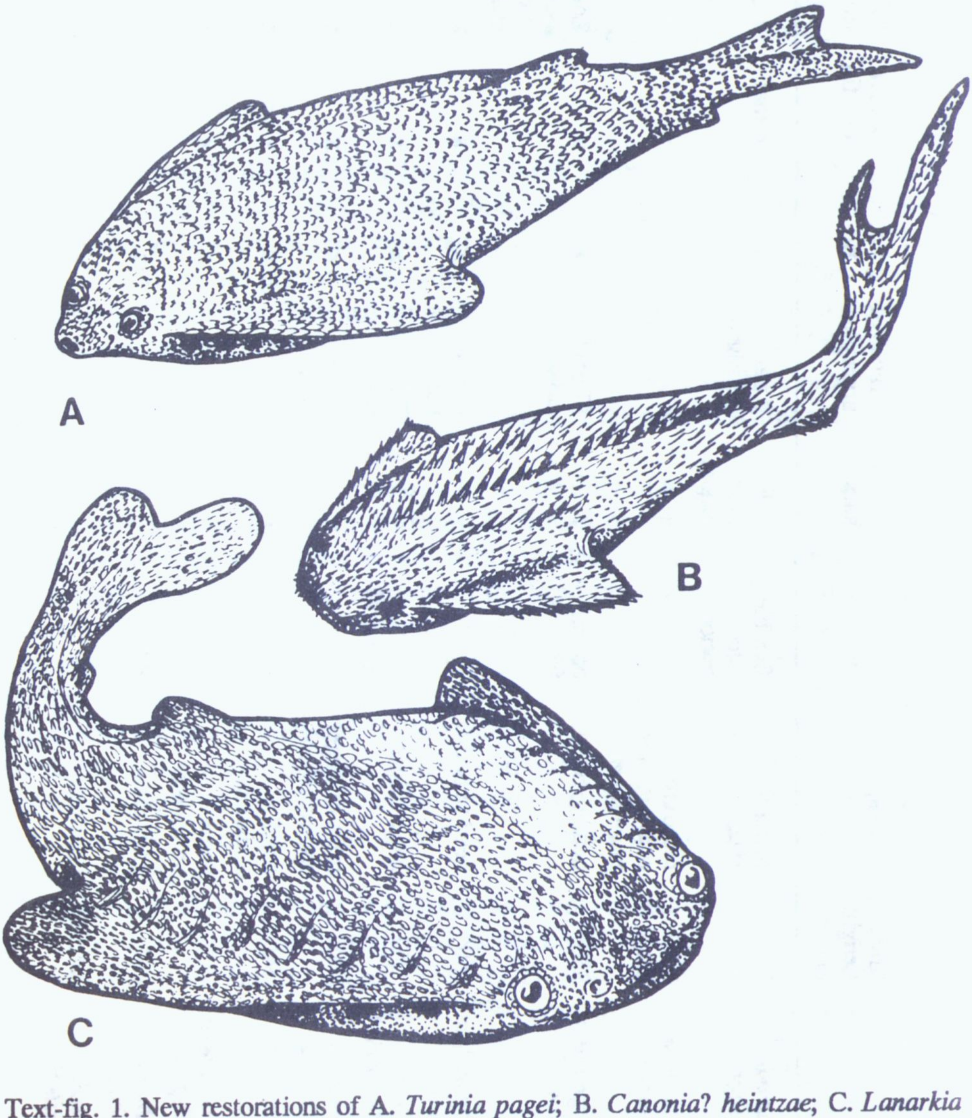
The internal skeleton of the cephalothorax is not yet clearly understood. Ridges and black stains have been interpreted as branchial structures in four thelodont species; ridges in *Turinia pagei* (Text-fig.1) were interpreted as a branchial apparatus by Powrie (1870). Traquair (1899a) pointed out that there were no actual gills or any sign of branchial opening and interpreted the ridges as a cartilaginous branchial skeleton, an idea which has persisted (e.g. Westoll, 1945; Turner, 1982). Westoll (1945) thought the arrangement showed gills with "ghosts" of endocranial

TABLE. Comparison of the general morphology of thelodonts based on complete specimens and partial squamations.

	Max. Lenght in mm	Scales	Head	Nasal sacs	Branchial apparatus	Pectoral fin	Dorsal/ anal fin	Caudal fin	Pore Canal System	Trunk
Turinia pagei	360	different sizes	flexible buccal region	pair near mouth	8 pairs of ridges	x	x anal	x	through scales in part	oesophagus
Thelodus parvidens	400 Est. 1 m	*bicostatiform* *trilobatiform* *pugniform*		–	–	–	–	–	?	–
Loganellia scotica	330	head to body	buccal fenestra	?	(7 or) 8 pairs	x	x	Zoned tail, symmetrical in older individuals	–	notochord myotomes
Loganellia taiti	150	head to body	–	–	(7 or) 8 pairs	x	x	x	–	–
Lanarkia "horrida"	75	large spines	buccal fenestra?	–	7 or 8 pairs	x	x	x	–	–
Lanarkia spinosa	130	rows of larger spines among	–	–	7 or 8 pairs	x	x	x	–	–
Lanarkia spinulosa	90	small spinelets	–	?	?	x	x	x	–	–
Phlebolepis elegans	75	some imbricate	rostral area	–	?	x	x	x	trough scales	–
Canonia? heintzae	150	imbricate	buccal fenestra?	–	–	x	–	–	? sensory line	–
Nikolivia milesi	Est. 205	imbricate	–	–	–	x	–	–	through scales in part?	–

structures. Stensiö (1958, 1964) envisaged nine pairs of visceral arches with extrabranchial atria; following Traquair, he thought that the upper surface of the holotype was dorsal, the median ridge then being the medulla. Westoll (1945) interpreted the ridge as the mid-aortic groove. However, if the surface is actually ventral or a mixture of dorsal and ventral squamation (see Turner, 1982), the ridge may represent the oesophagus and the midline confluence of the cartilaginous arches.

Traquair (1905), Stetson (1931) and Ritchie (1968a) found evidence of the branchial apparatus in *Loganellia scotica.* The pattern is similar to that in *Turinia*



Text-fig. 1. New restorations of A. *Turinia pagei*; B. *Canonia*? *heintzae*; C. *Lanarkia spinosa.* Post- pectoral and tail of C hypothetical.

pagei, with seven or eight pairs of subrectangular spaces separated by bars (Text-fig. 1A) which are thought to be interbranchial ridges, following Westoll (1945). Stetson figured *Loganellia taiti* (wrongly labeled "*Thelodus planus*" by Westoll, 1945, fig. 4c) with eight sub-rounded cartilaginous patches which may be the remains of the branchial pouches. Ritchie (1968a) claimed to have found evidence of eight possible branchial apertures forming a condensed row just below the pectoral flap. At least one specimen of *Phlebolepis elegans* seems to possess a branchial apparatus similar to that of *Loganellia* (Turner, 1991).

The structure of the brain is unknown. Presumably, thelodonts had an uncalcified chondrocranium. Darkly stained areas around and behind the eye region in some *Loganellia* specimens might be cartilages of the eye and auditory capsules.

The slim, paired triangular flaps or fins extend from just behind the flanks of the cephalothorax at mid-height. They are often preserved folded against the head. The base of the fin was long and slender. These thin flaps were covered with scales and were undoubtedly flexible. The scales are packed in straight rows which may have had an internal fibrous or cartilaginous support. The scales on the leading edge are invariably thick or large, and closely packed, whereas those on the trailing edge are smaller or more slender, and more widely spaced, comparable with modern shark squamation (Turner, 1982).

Behind the cephalothorax the body is narrow. The trunk was probably rounded in cross section, becoming more laterally compressed near the slim caudal peduncle. A single dorsal and anal fin were present, often placed well back. The tail is large and strongly asymmetrical in most thelodonts, with a small epichordal lobe and a long, often whip-like, hypochordal lobe. The tail is considered hypocercal because of the disposition of dorsal and anal fins, and because some specimens show traces of the notochord extending into the lower lobe. The tails of *Turinia pagei*, and possibly Loganellia scotica, are more symmetrical. The tail was flexible, shown by the creases preserved in it, especially in the web joining upper and lower lobes.

Trunk myomeres have been found in *Loganellia scotica* (Ritchie coll.) preserved as regularly-spaced bands bearing scales bunched together during muscle contraction, a pattern resembling that of lampreys (Ritchie, pers. comm.) Trunk musculature impressions are also preserved in *Turinia pagei*. The gut is seen passing under the squamation in some specimens (Turner, 1984).

Thelodonts had a sensory pore-canal system. Gross (1968) described scales with penetrating canals and one or more large external pores on the crown in *Phlebolepis* and interpreted these as part of a simple sensory line and/or mucus-producing system which lay below the scales. He demonstrated that these canals did not disrupt the dentine, and deduced that they formed at the same time as, or before, the scale. T. Märss (1979) showed the regularity of pore-canal rows and system comparable with that of other agnathans and fishes, and homologous with that of cyathaspids. She described two pairs of parallel lines with commissures on the dorsal cephalothorax. Above the eyes and down the snout are supraorbital and lateral profundus lines; ventral to the head is one pair of lateral canals, and possibly commissures, with pairs of pores probably to service the branchial apertures. Other rows on the side of the body may connect dorsal and ventral lines. Short runs of pores appear in the dorsal tail region.

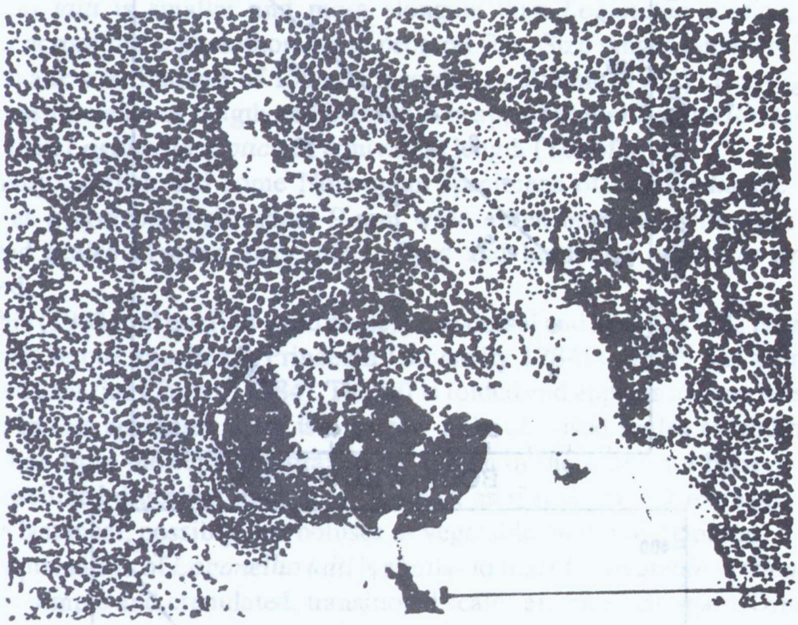
Pore-canal scales or sensory lines are known in other species (Karatajūte-Talimaa, 1978; Turner 1982; Dineley and Loeffler, 1976). In thelodonts with non-imbricating, loosely- packed scales the pore-canal system presumably developed without affecting the scales, although Vergoossen (1990) has suggested that ridges across the neck of some *Thelodus* scales represent the pore-canal location.

Loganellia scotica and *Loganellia taiti*

Traquair (1898, 1899a,b) was the first to investigate the gross morphology of thelodonts. From "*Thelodus scoticus*" (now *Loganellia scotica*) and *Lanarkia* species, then the oldest vertebrates known, he recognized the morphological unity of thelodonts. Additional material convinced Traquair (1901, 1905) of their agnathan status. Stetson (1931) recognized a new species, "*Thelodus*", now *Loganellia taiti*. Ritchie (1963, 1968b, c) and others (e.g. Hout, 1990) have brought to light new material from Scotland. Turner (1970) based her reconstruction of a thelodont on *Loganellia scotica*.

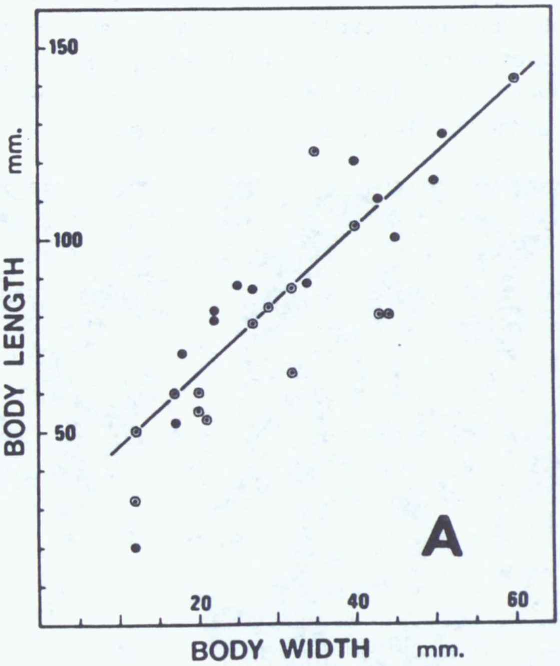
Loganellia scotica from the late Llandovery to early Wenlock fish beds of Lesmahagow and Hagshaw Hills is a primitive thelodont (Turner, 1990a, b), the oldest known from articulated material. Most specimens are less than 150 mm long, with maximum length estimated at 400 mm; measured specimens range from 52 mm to 330 mm in length (Text-fig. 3B). Larger specimens are indicated by detached caudal fins, which Ritchie (1963) found "surprisingly common". One such specimen led Traquair (1898) to erect a species "*Thelodus planus*", though Ritchie (1968c) doubted that this was a separate species. From more recent investigation (Turner, 1984), I suspect that Traquair was misled by a badly preserved specimen of *Loganellia scotica*. The scales he described (Traquair, 1898, p. 74) would certainly match those of *Loganellia scotica*. Besides the rather large flattened head and transitional scales, which Traquair (1898) said were "narrow, elongated and pointed posteriorly but without any strongly marked sculpture", there are more "normal" ridged body scales. The specimen is a mature individual whose scales had been eroded either during life, or post mortem. As Ritchie (1968c) suggested, and Turner (1976) reiterated, there is no reason to retain the name "*planus*".

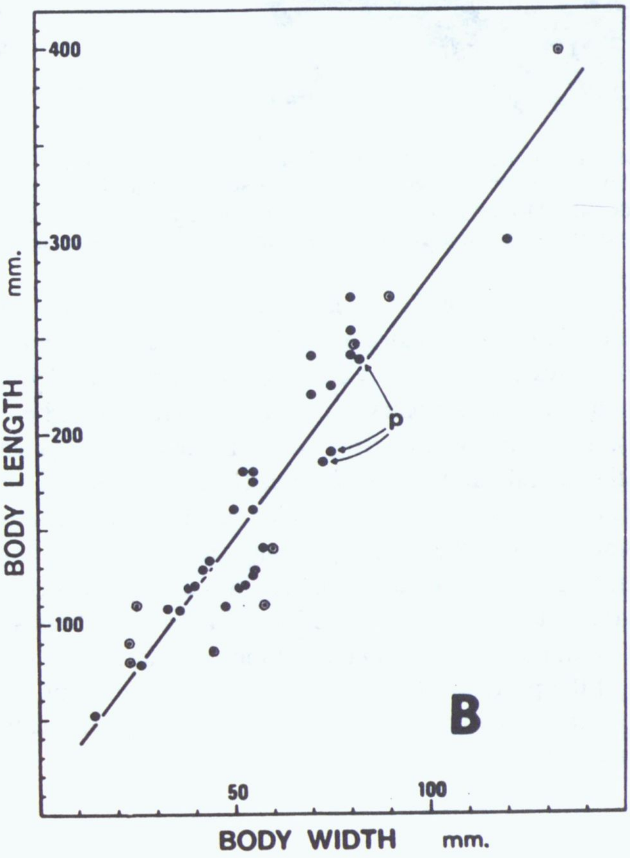
Thelodonts are commonly exposed in dorso-ventral view, with both upper and lower layers of the exoskeleton preserved. If one layer is removed, endoskeletal structures may be seen (Ritchie, 1963). The orbit in *Loganellia scotica* first noted by Traquair (1901, 1905), is about 7 mm in diameter and surrounded by irregular crenulate scales (Ritchie coll.). Ritchie (1963) photographed a well-preserved orbit; investigation of the blackstained eye (Text-fig. 2) reveals circular patches which look like holes but might be equivalent to the clear pigment, a feature of eyes in juveniles of other forms such as lungfish (Dr. Anne Kemp pers. comm.). The orbit is encircled by closely-packed scales which appear more blackened, suggesting underlying sclerotic cartilage. Near the orbit, possibly anterior to it, is a patch of loosely-packed scales with a distinct break in the squamation which might be a preservation artifact or represent the site of the efferent nasal duct. Another blackened area near the eyeball might be the otic capsule.



Text-fig. 2. Close up of eye region of *Loganellia scotica* to show style of preservation. Area to the lower left of and below the orbit with minute scales is the site of a possible nasal duct or spiracular opening. Drawn from a photograph taken by Dr A. Ritchie of a specimen in the Ritchie collection, Australian Museum, Sydney. Scale bar = approx. 8 mm.

The exoskeleton of *Loganellia scotica* is divided into three main parts; simple rounded and crenulated head scales grade into more elongate transitional scales, shaped like oak leaves, about midway along the cephalothorax. Typical body scales are navicular, with one or two pairs of crown ribs (Traquair, 1899b; Gross, 1967; Ritchie, 1963). There are regular rows of crenulated scales dorsal to the mouth which mirror the rostral patch in *Phlebolepis* (Rithie, 1968a). In some specimens an elliptical area, sparsely covered with scales, extends from the mouth to midway along the ventral surface of the head appearing to form a flexible floor to the buccal region (Turner, in prep.). Oral and orbital cavities are surrounded by the simplest scales, each with up to 10 crown crenulations. The bases of head scales are rather square with a central pulp depression, as in thelodontid scales. The scales on the trailing edges of the pectoral fins are spine-like and seem to be the longest body scales. Those on the unpaired fins are smaller. Generally, the scales are arranged in a series of intercrossing rows.


A
BODY LENGTH mm.
150
100
50
BODY WIDTH mm.
20
40
60


B
BODY LENGTH mm.
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100
BODY WIDTH mm.
50
100
p

Loganellia taiti and *Lanarkia* species (see below) are commonly found together in the late Wenlockian fish beds of Hagshaw, Lesmahagow, and Lyne Water, Pentland Hills of Scotland. A loganellid, similar to *Loganellia taiti*, from the late Wenlock fish bed of Rudstangen, Norway, is being studied by Ritchie (1968b, pers. comm.), who thinks it is probably a new species.

These loganellids are medium-sized and more advanced than *L. scotica* with complex multispinose body scales (Stetson, 1931; Turner 1984, in press). *Loganellia taiti* is smaller and more elongate than *Loganellia scotica*, being narrower across the cephalothorax and pectoral fins. Size ranges between 50-130 mm, with a few individuals of 150 mm recorded by Ritchie (1963) (Text-fig. 3A). From measurements of length and breadth it is apparent that *Loganellia taiti* was broader than *Loganellia scotica* of equivalent length (Text-fig. 4).

In many Scottish and some Norwegian specimens of *Loganellia* the mouth appears as a horizontal slit about 9 mm wide, often bordered with subcircular crenulated scales (Turner, pers. obs.). Eyes and branchial structures are also preserved.

Ritchie (1963) did not find good evidence of dorsal and anal fins in *L. taiti*. They are present in one specimen (Princeton University 12841), which has a fine tail, dorsal and anal fins (Turner, 1984). The tail is folded and appears to have been very flexible. In this specimen there is a narrow strip of raised scales extending in a sinuous line from the cephalothorax to the region of the anal fin. I believe this to be the fossilized digestive tract; it is "lumpy", as if it contained remnants of the animal's last meal, possibly soft boluses of vegetable matter or plankton.

The squamation of *Loganellia taiti* is similar to that of *Loganellia scotica*. Head scales are simple and crenulated; transitional scales are more elongate. Orbits and the terminal elliptical mouth are outlined with head scales (Ritchie, 1963, Pl. 10). The body scales, however, as Stetson (1931, fig.) discovered, are very distinctive (Turner, 1984, 1991, in prep.); the crowns can be very high and deeply grooved. Some bear one posterior crown point, but most have three to five, and up to seven

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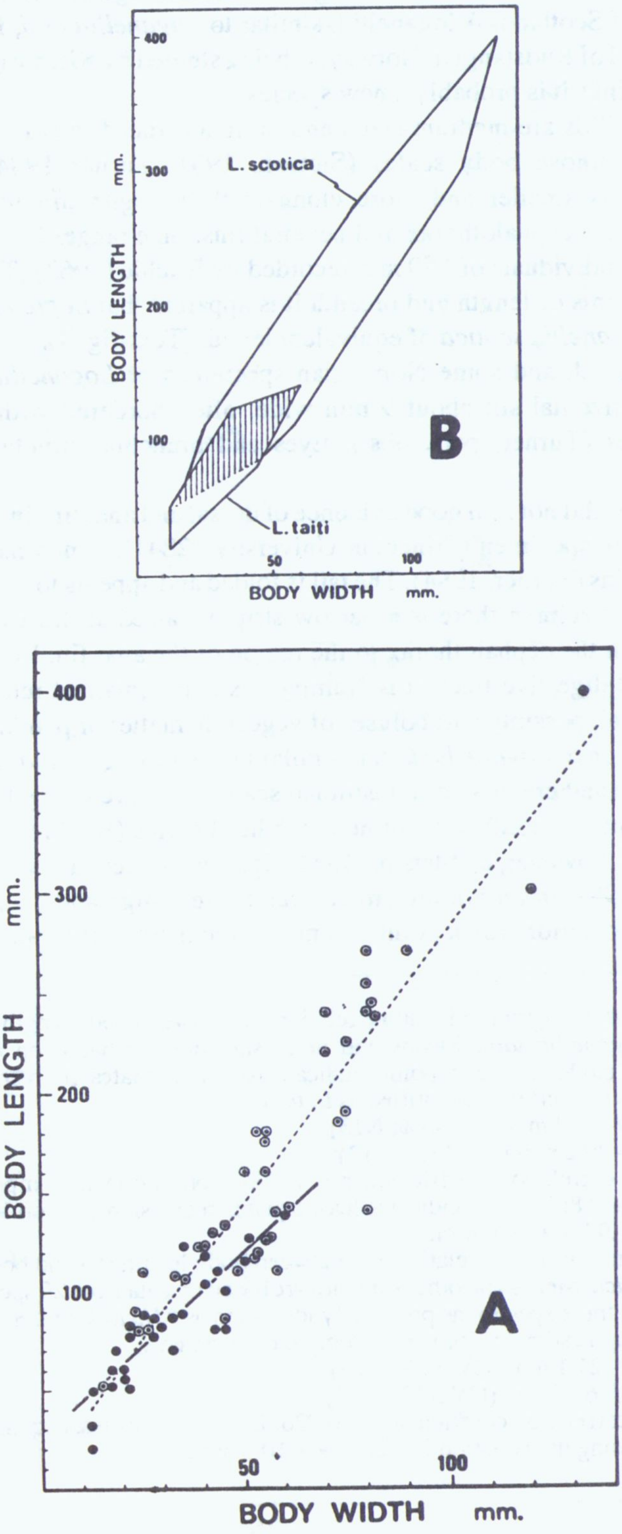
Text-fig 3. A) Scatter diagram to illustrate relationship between body length (L) and body width (W) in *Loganellia taiti*. Means and other statistics are based on data from 13 specimens (solid circles); ringed points indicate rough estimates for very incomplete specimens or ones not certainly identified as *L. taiti*
Mean W = 31.2 +/- 13.3 mm (CV 43%; N13)
Mean L = 87.5 =/- 29.2 mm (CV 33%; N13)
Product Moment correlation coefficient, r = 0.896 (correlation not improved by log transformation, r + 0.867). Line indicates least squares regression of L on W, expressing the equation L = 1.97W + 26.0 mm.
B) Scatter diagram to illustrate relationship between body length (L) and body width (W) in *Loganellia scotica*. Means and other statistics are based on data from 29 specimens (solid circles), including three specimens previously identified as "*Thelodus planus*" (p); ringed points indicate rough estimates for very incomplete specimens.
Mean W = 57.5 +/- 21.1 mm (CV 37%; N29)
Mean L = 165.7 =/- 61.5 mm (CV 37%; N29)
Product moment correlation coefficient, r = 0.926. Line indicates least squares regression of L on W, expressing the equation L = 2.71W + 10.0 mm.


400
300
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BODY LENGTH mm.
L. scotica
L. taiti
B
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BODY LENGTH mm.
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BODY WIDTH mm.

points. Short or long anterior spurs are present on most bases Gross (1967) did not figure these spinous body scales; those he did figure look like scales of *Loganellia scotica*. Scales also referred to *L. taiti* by Märss (1986, Fig. 11) do not resemble those of the holotype.

Lanarkia species

Traquair (1898) differentiated three species of these spiny thelodonts, *Lanarkia horrida*, *L. spinosa* (Text-fig. 1C) and *L. spinulosa* on their different-sized spines. He found the "contour of head, body, tail and fins as in "*Thelodus*", and the "dermal armature consisting of small, sharp, conical spines, hollow within and widely open below, without basal plate". This last statement is not quite correct, for he was examining young scales; older scales with a rounded thickened base and a single pulp hole can be found (Text-fig. 5).

In this investigation I found no apparent difference between *Lanarkia horrida* and *L. spinosa* except size (Text- figs 6, 7); as larger specimens are examined, the scale pattern of the "horrida" form grades into "spinosa" form. *Lanarkia spinulosa* does have different, relatively tiny scales. Specimens in the Ritchie collection show that some head scales in the "horrida" form are identical with *Thelodus traquairi* Gross, 1967 (Fig. 5), thus confirming the thelodontidid nature of *Lanarkia* scales. *Lanarkia* is thus related to *Thelodus* and not to loganiids as it was earlier supposed on morphological grounds (Turner, 1976).

The three *Lanarkia* species of Traquair (1898) are all small and show a size gradation (Text-fig. 7) which might represent a growth series; the "horrida" specimens are below 60 mm in length, most *Lanarkia spinulosa* specimens are around 85 mm, and *Lanarkia spinosa* and some *Lanarkia spinulosa* specimens may reach 200 mm. *Lanarkia horrida* is consistently small, with a large cephalothorax and very large trumpet-shaped spines; Ritchie (1963) suggested that the larger spines in *L. spinosa* are only on the dorsal side. In some specimens of the "horrida" form (e.g. SMA38265, Turner, 1991), smaller spines can be seen fringing the buccal margin. The smallest specimen seen is 13 mm long; rarely do they reach 60 mm. Remains from Slot Burn, around 20-30 mm in length, (Ritchie, 1963) possess large carbonized eye spots and are probably juvenile stages. Larger specimens, usually labeled *Lanarkia horrida*, are invariably *L. spinosa*, which ranges from 6o to 160 mm in length. Its squamation is composed of very large spines (up to 2.5 mm) interposed in a network of closely-spaced smaller ones. All spines have ribbed ornament (Text-fig. 5). In the specimens ranging from 60 to 85 mm, small spines can be seen on the front of the head, with larger ones over the rest of the body.

Text-fig 4. A) Comparison of body proportions in *Loganellia scotica* (solid circles) and *Loganellia taiti* (ringed points). For each species the line indicates regression of body length on body width (continuous line - *L. taiti*; dashed line - *L. scotica*). Based on data in Text-fig. 4.
B) The same comparison (reduced scale) with distribution for each species indicated by minimum convex polygon. Shading indicates zone of overlap between the two distributions.

As *Lanarkia horrida* grew, small spines were added into the squamation between the larger beginning from the anterior (SMA38265, PU14101, Turner 1984).

Lanarkia spinulosa is the rarest form and the largest *Lanarkia*; weathered specimens are difficult to distinguish from poorly preserved specimens of *Loganellia taiti*. According to Ritchie (1963), fragmentary remains indicate a maximum length of around 200 mm. Specimen SMA38286 exhibits size range and differential spacing of scales, with fewer and larger scales in the centre of the head, and smaller thin scales on the trailing edges of the pectoral fins. AMNH6926 exhibits the broad head, with a mouth of around 5 mm wide flanked by two small hemispherical concavities, 1-2 mm across, which may mark the location of nasal sacs.

Lanarkia scales are arranged in regular rows which were easily disarranged by post-mortem flattening. One specimen (SMA38266) even shows the spines pointing anteriorly. Larger spines often have anterior basal processes to anchor the scales into the dermis. Possibly the spines were mobile, perhaps even erectile, during life. As a viable defence mechanism they might even have been toxic. The large spines on cephalothorax and, in some, down the dorsal midline of the trunk in *L. spinosa*, were arranged in close parallel rows. Individual variation seems likely (Turner, 1991).

The posterolateral tips of the pectoral flaps are angular in *Lanarkia* species. Scales on the trailing edges of fins are smaller, or more slender, and loosely-packed, as in other thelodonts. The mouth is often well preserved (see Stetson, 1931, Fig. 4). Stetson (1931) figured the "horrida" form with a ring of closely-set, thorn-like scales underlain by black carbonaceous material which he interpreted as a cartilaginous support for the mouth.

Measurements

Scottish Silurian thelodonts were measured to discern any pattern of variation within and between the species. The range of lengths and widths of specimens is shown in Text-figs 3, 4, 6 and 7. (A list of measured specimens is given in Turner, 1984). Total length of a specimen is taken from the most anterior point of the squamation to the most posterior point of the tail (if present). Breadth is taken as the maximum width across the specimen, usually between the lateral margins of the pectoral fins. Total length of an incomplete specimen can be estimated if the fossil is not too distorted, by assuming that cephalothorax and tail both are approximately equal to one-quarter of total length. Estimates tend to be quite close (within 10 mm) of the predictions from regression analysis.

Length has been plotted against breadth for each species. The width measurement was deliberately chosen as the independent variable; this is because

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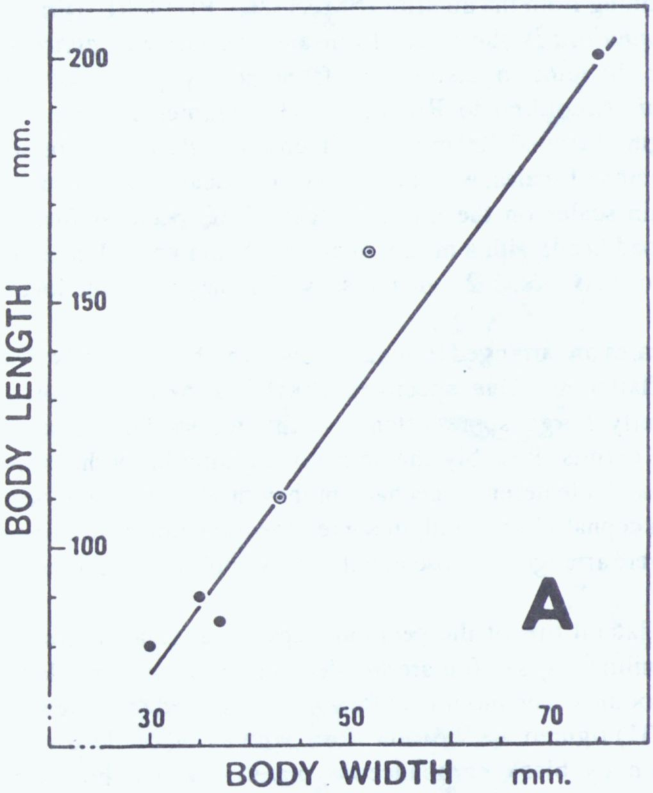
Text-fig. 5. Variation in scale form of Lanarkia spinosa, including some of the oral and cephalo-pectoral scales which are identical to the *"Thelodus traquairi"* form of Gross (1967) (scale illustrations after Gross, 1947).


BODY LENGTH mm.
200
150
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30
50
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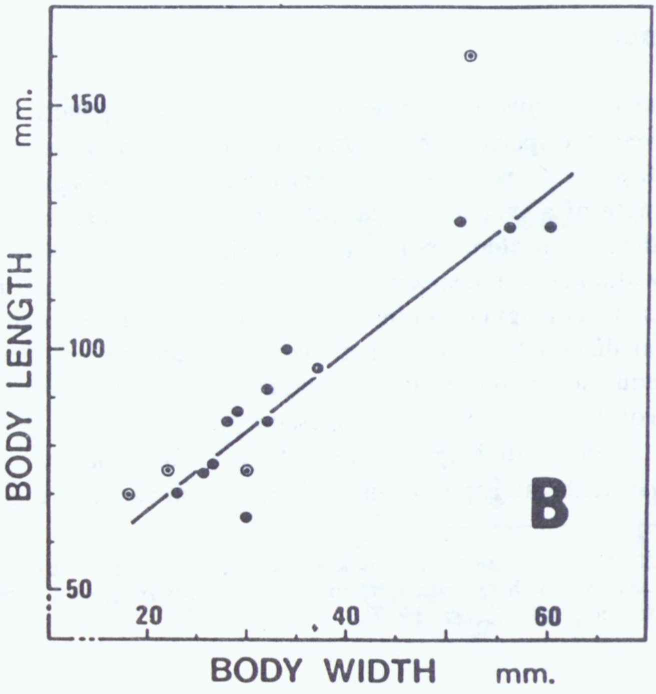
BODY WIDTH mm.
A


BODY LENGTH mm.
150
100
50
20
40
60
BODY WIDTH mm.
B

an incomplete specimen usually provides a good measurement of width, whereas its total body length may more commonly be affected by damage. The diagonal line drawn on the graphs represents the least-squares regression of length on width; prediction of the length is therefore possible if the width is known. The product moment correlation coefficient is given as a measure of association between length and width.

Mean length and width are shown with standard deviation and coefficient of variation (i.e. standard deviation expressed as percentage of mean). Length can be predicted with the formula given for each species, l = slope w + intercept. All measurements are in millimetres.

Graphs for *Loganellia scotica* (Text-fig. 3B, 4) and *Loganellia taiti* (Text-fig. 3A, 4) have very different lines of regression. The area of overlap falls below 140 mm length. The three *Lanarkia* "species" were plotted separately (Text-figs 6A, B, 7A), and then in a combined graph (Text-fig. 7B). The regression lines for the "horrida" form and *Lanarkia spinulosa* are similar in slope. As noted from observation, there is a zone of transition between the "horrida" and "spinosa" forms, from 60 mm to about 80 mm in length. Animals within this range cannot be placed definitely into either form. From the regression line of *Lanarkia spinosa* it appears that the proportions of length to width altered as the animal grew, the cephalothorax becoming relatively broader. Only a small sample was available for measurement, especially in *Lanarkia spinosa* and *L. spinulosa* but enough to substantiate the general observations that the "horrida" form and *Lanarkia spinosa* were different growth stages. Was *Lanarkia spinulosa* a growth stage, or possibly a sexual dimorph of *Lanarkia spinosa*?

Turinia pagei (Text-fig. 1A)

The holotype (Turner, 1982) is about 360 mm long and a second specimen from Mitcheldean is estimated to have been equally as long (Turner in Allen et al., 1968). The tips of the pectoral flaps are rounded with large robust scales on the leading

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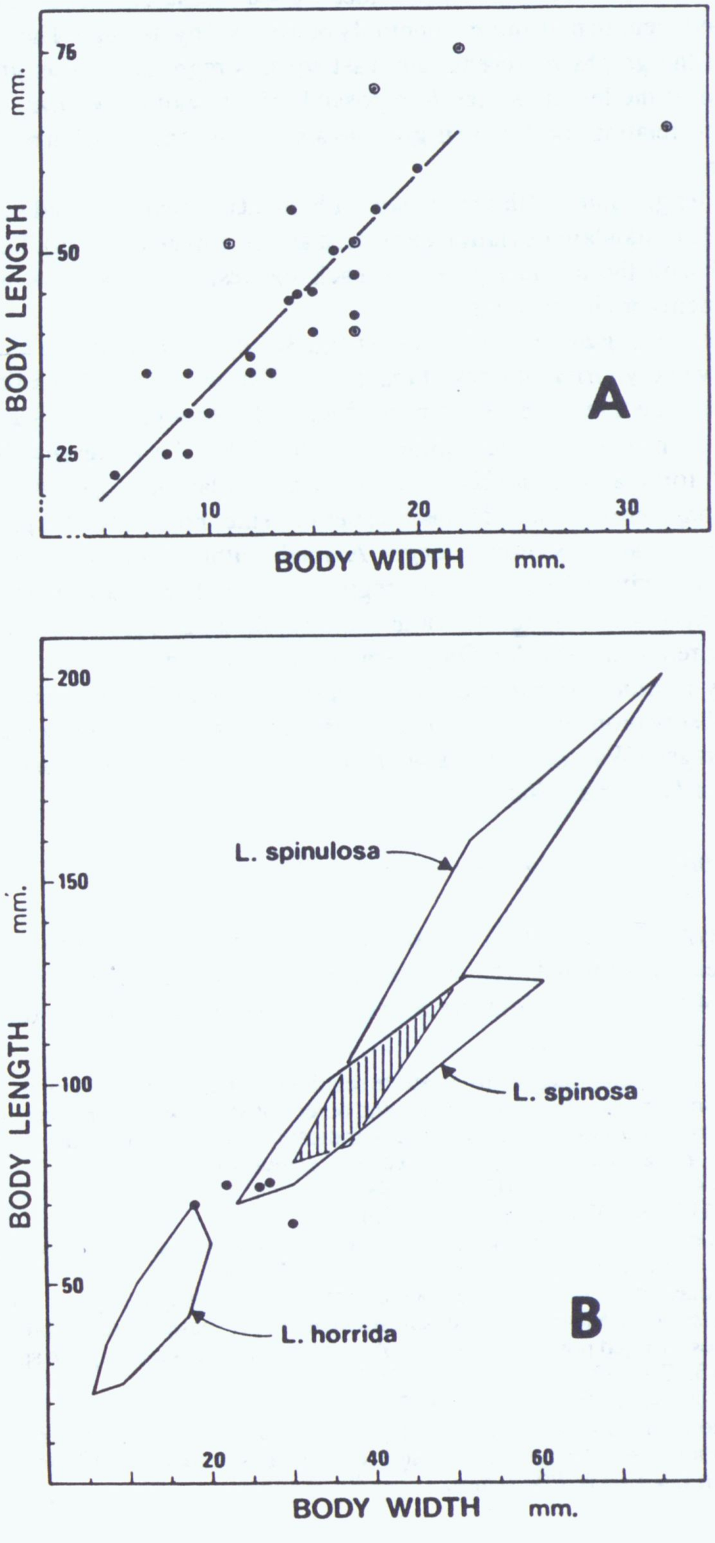
Text-fig. 6. A) Scatter diagram to illustrate relationship between body length (L) and body width (W) in *Lanarkia spinulosa*. Means and other statistics (below) are based on data from 4 specimens (solid circles); ringed points indicate rough estimates for very incomplete specimens or ones not certainly identified as *L. spinulosa*.
Mean W = 44.3 +/- 20.7 mm (CV 47%; N4)
Mean L = 113.8 =/- 57.6 mm (CV 51%; N4)
Product moment correlation coefficient, r = 0.994. Line indicates least squares regression of L on W, expressing the equation L = 2.77W - 8.7 mm.
B) Scatter diagram to illustrate relationship between body length (L) and body width (W) in *Lanarkia spinosa*. Means and other statistics (below) are based on data from 13 specimens (solid circles); ringed points indicate rough estimates for very incomplete specimens.
Mean W = 35.7 +/- 12.1 mm (CV 34%; N13)
Mean L = 92.8 =/- 21.2 mm (CV 23%; N13)
Product moment correlation coefficient, r = 0.936 (correlation not improved by log transformation, r + 0.919]) Line indicates least squares regression of L on W, expressing the equation L = 1.63W + 34.6 mm.


BODY LENGTH mm.
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BODY WIDTH mm.
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BODY LENGTH mm.
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60
BODY WIDTH mm.
L. spinulosa
L. spinosa
L. horrida
B

edge and small loosely-packed scales on the trailing edge and the bulk of the distal flap (Turner, 1982). A vase-shaped mound behind the mouth is probably the infilled buccopharyngeal space. Behind this is a median ridge, perpendicular to which is a paired series of eight posteriorly-curving ridges extending almost to the lateral margin of the cephalothorax. The sparseness of scales covering all these areas may be a consequence of post mortem dispersion. General branchial structure is discussed above. Distal to each of the ridges, and internal to the pectoral flap, there are patches of scales, smaller than normal head scales, which may have covered flaps over the branchial openings. Evidence of rather rectangular branchial chambers was found in the Mitcheldean specimen (Allen et al., 1968). *Turinia pagei* had an anal fin, a small rounded dorsal fin, and a tail which appears almost symmetrical, with more rounded lobes. The general form is very reminiscent of modern squatinids in which the tail is almost symmetrical with the notochord just turning down into the lower lobe (Bigelow and Schroeder, 1948).

Nikoliviids

The other reasonably complete specimens which have come to light are nikoliviid thelodonts. Turner (1982) described *Nikolivia milesi* from the Dittonian of the Welsh Borderland, the single specimen of which was estimated to be about 205 mm in length. Dineley and Loeffler (1976) named *Sigurdia heintzae* from the Early Devonian of Arctic Canada. In 1982 Turner also referred *S. heintzae* tentatively to *Nikolivia* principally because the scales portrayed by Dineley and Loeffler were of nikoliviid type. The Arctic Canadian nikoliviids should possibly belong to the genus *Canonia* Vieth, 1980 because of their scale morphology. The length of the holotype of *Canonia*? *heintzae* (Dineley and Loeffler, 1976, pl. 22) is estimated to have been no greater than 120 mm. There are ten specimens in all which indicate body shape in *Canonia*? *heintzae* ranging from 100 to 150 mm in length, and around 30 mm across the pectoral fins (Turner, pers. obs.). All are flattened dorso- ventrally (Text-fig. 1B). The posterior cephalothorax is broad, narrowing anteriorly to an elongated mouth region. The buccal region is sparsely covered with slender scales. Head and transitional scales are rounded, grading into more elongate, lanceolate

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Text-fig. 7. A) Scatter diagram to illustrate relationship between body length (L) and body width (W) in *Lanarkia spinosa* "horrida" form. Means and other statistics (below) are based on data from 20 specimens (solid circles); ringed points indicate rough estimates for very incomplete specimens.
Mean W = 13.1 +/- 4.1 mm (CV 31%; N20)
Mean L = 41.2 =/- 12.5 mm (CV 30%; N20)
Product moment correlation coefficient, r = 0.866. Line indicates least squares regression of L on W, expressing the equation
L = 2.65W + 6.6 mm.
B) Comparison of body proportions in the three species of *Lanarkia* named by Traquair. Distribution for each species is indicated by minimum convex polygon; shading indicates zone of overlap between distributions. Solid circles indicate specimens which are transitional in squamation morphology between *Lanarkia spinosa* "horrida" form and *Lanarkia spinosa*.

body scales around the level of the anterior pectoral flaps. The latter are small and narrow, with rounded posterior tips. No sign of eyes or branchial structures has been found. The body narrows behind the cephalothorax. The unpaired fins and the caudal region are not preserved. Immediately behind the pectoral flaps on the lateral margin of the body the denticles are stouter and slightly larger than other body scales. Traces of canals near the lateral margin of NMC13754, reported by Dineley and Loeffler (1976), might be the result of infolding of the squamation, or the trace of a sensory line system. No pore canal scales have been seen the presence of which would be expected in a thelodont with an imbricated squamation.

Conclusions

The majority of smaller thelodonts, some loganellids, *Lanarkia* and *Phlebolepis*, seem to have been well- adapted for surface swimming, capable of filter-feeding as they swam along. With eyes placed well-forward, a terminal mouth, a full complement of fins and a good sensory system, including their complex sensitive squamation, they must have been very manoeuverable. From the fin configuration, with unpaired fins placed well back near the tail, such thelodonts must have been good swimmers, capable of darting. The cephalothorax, although large, was probably not a heavy structure, being essentially a buccopharyngeal basket with uncalcified cartilaginous bars with overlying uncalcified braincase. The thelodont must have been able to rise up through the water by inclining the pectoral flaps and raising its head slightly. The hypocercal tail must probably have helped to counteract the cephalothorax when descending to the bottom.

Lanarkia seems most specialized with its complete covering of spines. Young *Lanarkia* resemble puffer-fish, making use of a defensive, possibly erectile, spine system. The adult *Turinia pagei* was almost certainly a bottom-dwelling animal. At least one modern shark and some of the rays bear a strong resemblance to *Turinia*. Squatinids have a definite thelodont "look" with a large cephalothorax and branchial openings below and only slightly to the side of the split pectoral fins. It is the only living shark to possess a near- hypocercal tail with the lower lobe longer than the upper one and the caudal axis below the main trunk axis. *Canonia*? *heintzae* was probably a specialized feeder, possibly a bottom-dweller, with a sucking tube-like mouth.

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The structure of growth layers of Silurian fish scales as a potential evidence of the environmental changes

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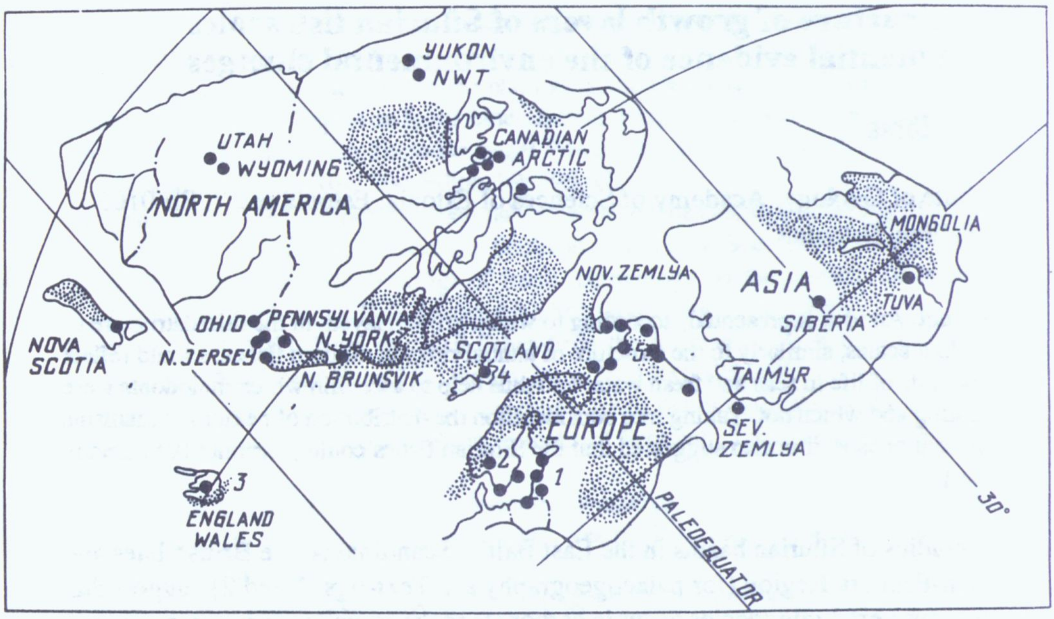
Abstract. An idea is presented, according to which growth layers in the microstructure of thelodont scales, similarly to the structure of annual rings in modern fishes, should reflect the periods of life in seas and fresh water and thus help to ascertain which thelodonts were migrating and which not. Taking into consideration the distribution of nektonic organisms in present oceans, it is also suggested that the Silurian fishes could distribute latitudinally as well.

The studies of Silurian basins in the East Baltic, Scandinavia, the British Isles and Timan-Pechora Region (for palaeogeography see Text-figs. 1 and 2) suggest that numerous vertebrate species occur in carbonate rocks as well as in terrigenous ones (Text- fig. 3). Vertebrate-bearing clastics are often considered to be sediments of fresh- or brackish-water deltas, estuaries, near- shore bays, lagoons, continental stream channels or tidal flats, while carbonates are mostly regarded as marine deposits. Detailed studies in this field have been carried out by Romer and Groove (1935), Gross (1950), Denison (1956), Robertson (1957), Allen and Tarlo (1963) and also by Mark-Kurik and Märss (1991).

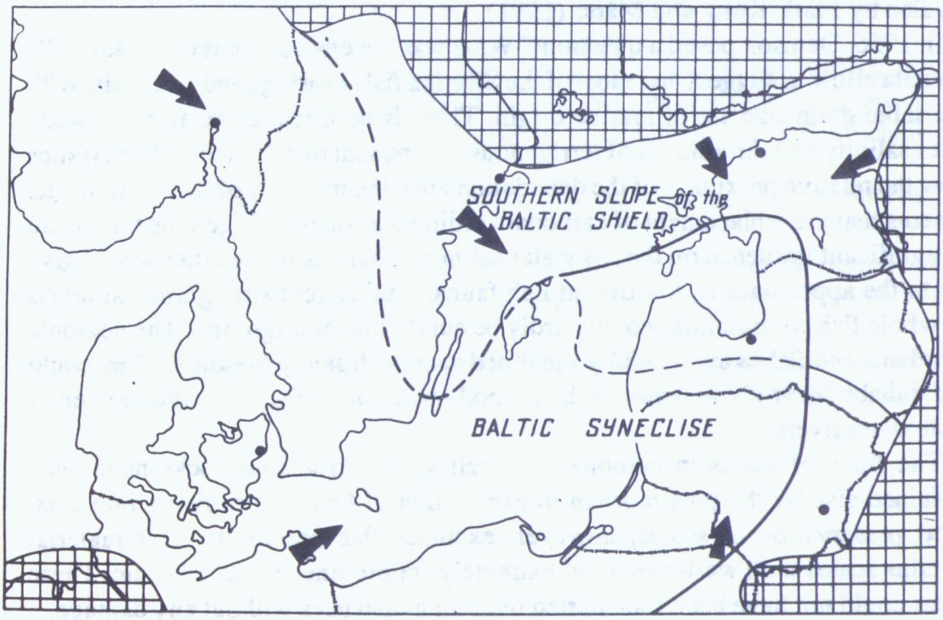
In 1956, Denison posed a question: "What was the environment of the sands?". Our data allow to suggest that most of the Silurian fish-bearing sandy deposits with a variable grain size are of marine origin. There is no direct correlation between water salinity and the amount of terrigenous component of sediments. The clastics show the relative proximity of the denudation area, the intensity of denudation, etc. It seems that the replacement of carbonate sedimentation by terrigenous facies had no significant influence on the sea water salinity. Changes in the latter would give rise to the appearance of a different fish fauna. At different stratigraphical levels the whole fish communities could hardly be euryhaline or migrating. The nektonic agnathans and fishes successfully inhabited seas with sandy bottoms. They could also inhabit near-shore areas rich in food, but, probably, they did not enter fresh-water rivers.

The finds of scales in carbonate as well as in terrigenous rocks have been explained also by the post-mortem transportation of fishes from rivers into seas. Good preservation of scales, however, excludes this possibility. Our material contains scales with well-preserved extremely fragile fine spines, ribs, etc. These scales could not have been transported over long distances without any damage.

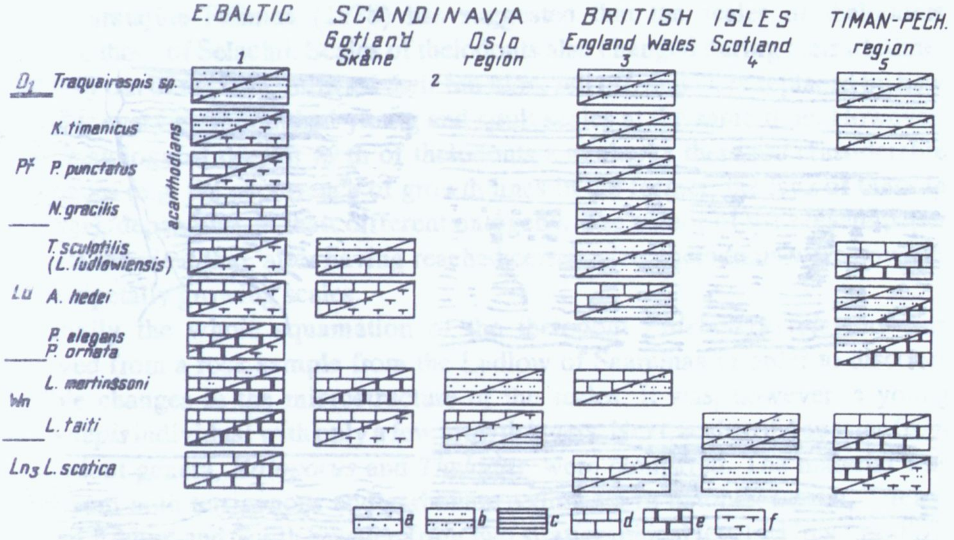
The problem concerning the mode of life of Silurian fishes is open to debate: did they migrate and which of them were adapted to the life both in fresh and saline



Text-fig. 1. A partial overview of Silurian global palaeogeography (after C.R. Scotesė et al., 1979). Solid circles show vertebrate distribution areas: 1 - East Baltic and Poland; 2 - Scandinavia; 3 - Southern Britain; 4 - Scotland; 5 - Timan-Pechora Region. Stippled areas indicate probable land.



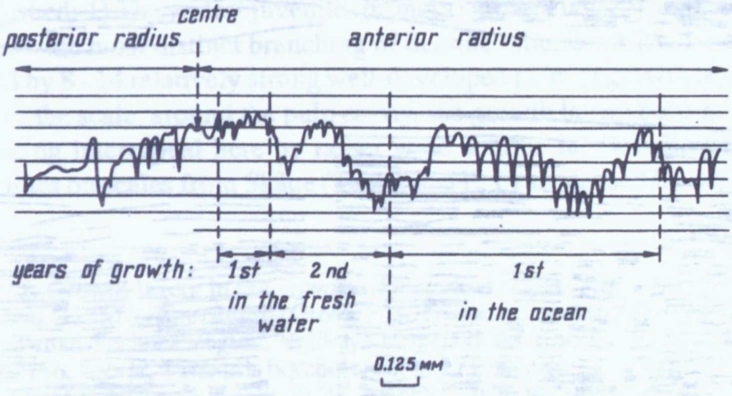
Text-fig. 2. Palaeogeography of Baltic area (after Jürgenson, 1988).



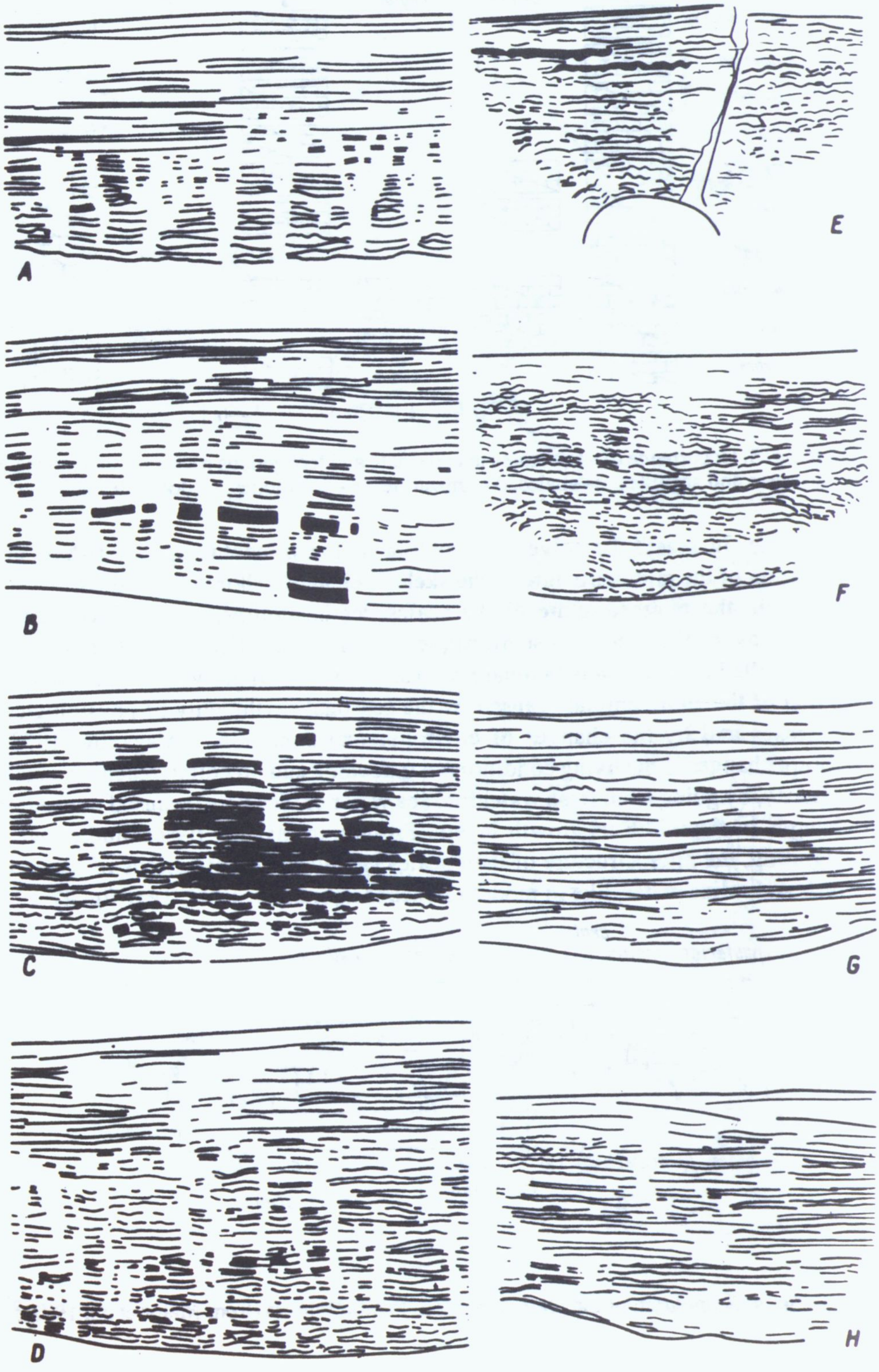
Text-fig. 3. Occurrence of vertebrates in carbonate and terrigenous rocks. a - sandstones, b - siltstones and argillites, c - shales, d - limestones, e - dolostones, f - domerites and marls.

water (i.e. in seas)? To solve the problem of the palaeobiology of fishes, the formation of the microstructure of the skeletal elements should be studied.

Within the microstructure of the scales, teeth, otoliths, etc. of fossil fishes hyaline layers alternate with semiopaque ones. In recent fishes the alternation of the so-called growth layers (annual rings) shows seasonal growth of scales as well as that of the entire animal "caused by the seasonal rhythmicity of physiological processes and by the changes of environmental conditions" (Vaganov, 1978). Abrupt changes in the living conditions, e.g. feeding and breeding (reaching sexual maturity, by going from fresh water into sea water or vice versa) caused noticeable changes in the width of growth layers. Presuming that the fishes studied were migrating, the microstructure of their scales should represent periods of living in fresh and saline water, like in modern fishes (Major et al., 1972; Text-fig. 4).



Text-fig. 4. Scanogram of the scale of modern Pacific salmon (from Major et al., 1972).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V. Karatajūte-Talimaa (1978) has suggested that the scales of thelodonts resemble those of Selachii. Scales of thelodonts also changed during their lifetime: they grew out of the skin, fulfilled their function, fell off, and were replaced by new ones. So, every thelodont had young and adult scales at the same time. However, in the histology of dermal teeth of thelodonts and sharks there are considerable differences (e.g. the occurrence of growth lines in the former, the lack of them in the latter), depending on their different ontogeny. The author of the present paper supports the view that, after having reached certain size, thelodonts were covered by centripetally growing scales.

Initially the whole squamation of the thelodont *Phlebolepis elegans* was dissolved from a rock sample from the Ludlow of Saaremaa in order to discover possible changes in the microstructure of the scales. It was, however, a young *Phlebolepis* individual with only a few growth layers. Next, scales of 4 species from 2 thelodont genera, *Katoporus* and *Thelodus*, were compared. The material was taken from both terrigenous and carbonate sediments in Estonia, Latvia, Timan-Pechora Region and South Sweden from two stratigraphical levels: Upper Ludlow and Upper Pridoli. All the scales came from the same climatic belt of the Silurian (see Text-fig. 1). For the thin section the thickest scales possible were chosen, as scales of older individuals yield considerably more information.

***Katoporus* scales.** The growth layers are arranged regularly in the crowns, interrupted only by pulp canals, dentine tubules and canals. Growth lines are not straight but slightly convex at the canals (Pl. I figs. 1-5; Text-fig. 5 A-D). The relatively wider growth layers of the upper part of the crown become slightly narrower in the lower part. The maximum number of hyaline and semiopaque layers was:

Katoporus timanicus from siltstones of Timan - 41 layers, *K. timanicus* from limestones of Latvia - 51 layers.

***Thelodus* scales.** Growth layers run parallel to the outer surface of the scales. They are best developed in the middle of the crowns, dispersed on the neck and in the base, and lacking in the basal layer (Pl. II figs. 1-4; Text-fig. 5 E-H; see also Gross, 1967, Fig. 1, 2). In the scales from Estonia and Skåne three zones can be distinguished: 1) The widest juvenile (primary) growth layer. The lower surface of this shows the most distinct branching of dentine tubules. 2) The juvenile layer is followed by 8 - 14 relatively strong well-developed pairs of growth layers. 3) In the middle of the scale, around the pulp cavity, the growth layers become less distinct again, being interrupted here by rather wide dentine tubules. Broken and wavy growth lines on scales from Skåne (Text-fig. 5 E, F) are caused by dentine tubules,

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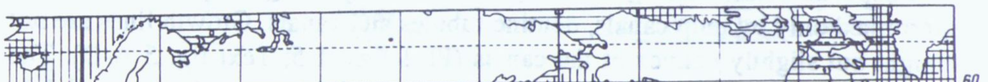
Text-fig. 5. Growth layers in the crowns of thelodont scales: A-D - *Katoporus timanicus* Kar.-Tal.; E,G - *Thelodus sculptilis* Gross; F,H - *Thelodus parvidens* Agassiz. A,B - Pi 7153, Pi 7154, Timan-Pechora Region, Velikaya River, borehole no 385, depth 329 m; C,D - Pi 7155, Pi 7156, Latvia, Ventspils borehole, depth 273.6 m; E,F - Pi 7157, Pi 7158, Sweden, Skåne, Ramsåsa Beds; G,H - Pi 7159, Pi 7160, Estonia, Sakla borehole, G,H - depth 10.52-10.58 m.

and also as a result of diagenesis. The maximum number of hyaline and semiopaque layers was as follows:

Thelodus sculptilis from sandstones of Skåne - 32 layers
T. sculptilis from limestones of Estonia - 34 layers
Thelodus parvidens from sandstones of Skåne - 36 layers
T. parvidens from domerites of Estonia - 34 layers
Thelodus admirabilis from domerites of Estonia - 36 layers

All four species of both genera treated above are characterized by paired layers: a wider semi-opaque and narrower hyaline layers forming a cycle. The semi-opaque layers seem to be divided in turn but these layers are weakly visible under a small light microscope. The cycles provide evidence of growth differences at succeeding time intervals, e.g. day and night, summer and winter, but could be also caused by dry and rainy periods, ebb and flow, etc. Still, the latter cannot be taken into consideration, as the growth layers are too regular. Of certain significance is the type of climate where the basin with fishes was located. To this study are relevant the subequatorial and tropical belts. As in the subequatorial belt seasonal rhythmicity of natural processes is caused by the alternating rainy and dry periods, whereas in the tropics diurnal and nocturnal temperatures differ considerably, and



Text-fig. 6. Geographic distribution of some nectonic organisms in the World Ocean (after Aleyev, 1976, fig. 2). 1 - *Hirundichthys rondelettii* (Val.), 2 - Exocoetidae, 3 - Cheloniidae, 4 - *Boreogadus saida* (Lepechin) (the northen hemisphere) and *Pleuragramma antarcticum* Boul. (the southern hemisphere), 5 - Gonatidae, 6 - Spenisciformes. The thick lines mark the northern and southern limits of the distribution *Hirundichthys rondelettii*, which are also considered as boundaries between the different biogeographic realms (arctic-boreal, tropical and antarctic-notal).

the annual temperature curve is noticeable, the rhythmicity is caused by temperature differences. In both climatic belts a cycle of growth layers of scales seems to correspond to the year of growth. The scales, as well as the thelodonts themselves grew throughout the year, but during a part of the year the growth rate was lower. In the ontogeny of scales the most prominent, i.e. the widest, is the exterior layer. In modern fishes the growth of the whole fish as well as that of its scales slow down with the age (Vaganov, 1978), i.e. annual rings become narrower. This can be also observed in the scales of *Katoporus* (Text-fig. 5 A-D), considerably less in those of *Thelodus*.

At present it seems impossible to find more distinct levels in the microstructure of the scales of *Katoporus* which would correspond to abrupt changes in the living conditions of these fishes. In *Thelodus* scales this level could be in between the described zones. Exact measurements are needed to solve this problem; here only an idea is presented.

Aleyev (1976) provides interesting data on the geographic distribution of some nektonic organisms in the World Ocean (Text- fig. 6). If we compare it with the map of the climatic belts, we can see a clear dependence of the distribution of nektonic organisms on the climate. All the groups and species shown exist in an optimum climatic belt, adjacent zones act as a barrier to their distribution.

Climatic zonation has already been studied for some fossil groups. For example, acritarchs show a clear palaeolatitudinal distribution pattern related to water temperature (Dorning, 1989).

Keeping in mind the latitudinal distribution of recent nektonic organisms in oceans and seas, we should search for material that might establish the latitudinal distribution of Silurian and younger fishes. Basing on the palaeogeographical reconstructions of Scotese et al. (1979) and Scotese (1986) and biogeographic provinces by Aleyev (1976), we may assume that all Silurian fish localities of the East European Platform and adjacent areas are situated 40° south and north of the equator, i.e. they belonged to the tropical biogeographic realm.

Acknowledgements. I am greatly indebted to Mrs. Anne Noor (Tallinn) and Dr. David Harper (Galway) for linguistic help. Sincere thanks to Mrs. Ludmilla Lippert for skillful drawings, to Mr. Udo Veske and Mr. Erik Grünberg for photographs. The support was given by Sonderforschungsbereich (SFB) 230 "Natural Structures", Stuttgart, Tübingen.

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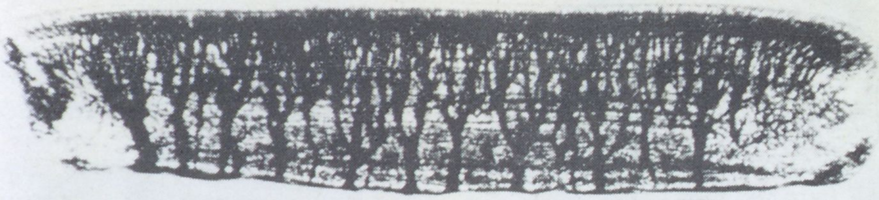
Plate I.
Structures of growth layers in the scales of thelodont *Katoporus timanicus* (Kar.-Tal.)
Figs. 1, 2. Scales from siltstone. Timan-Pechora Region, Velikaya River, borehole no 385, depth 329 m, Upper Pridoli, uppermost part of the Greben Regional Stage. Pi 7153, Pi 7154, x 100. Figs. 3-5. Scales from dolomitic limestone. Latvia, Ventspils borehole, depth 273.6 m, Upper Pridoli, Targale Fm, Luzni Beds, Pi 7155, x 125; Pi 7156, x 100; Pi 7162, x 130. The growth layers in the crowns of scales in figs. 1-4 have been presented also in Text-fig. 5A-D.

Plate II.
Fig. 1. *Thelodus sculptilis* Gross. Scale from sandstone. Sweden, Skåne, Upper Ludlow, Ramsåsa Beds. Pi 7157, x 140.
Fig. 2. *Thelodus parvidens* Ag. Scale from sandstone. Sweden, Skåne, Upper Ludlow, Ramsåsa Beds. Pi 7158, x 120.
Fig. 3. *Thelodus parvidens* Ag. Scale from domerite. Estonia, Sakla borehole, depth 10.52-10.58 m. Upper Ludlow, Kuressaare Regional Stage, Tahula Beds. Pi 6443, x 160.
Fig. 4. *Thelodus admirabilis* Märss. Scale from domerite. Estonia, Sakla borehole, depth 6.2 m. Upper Ludlow, Kuressaare Regional Stage, Tahula Beds. Pi 6333, x 200. The growth layers in the crowns of scales in figs. 1 and 2 have been presented also in the Text-fig. 5E, F.

Plate I



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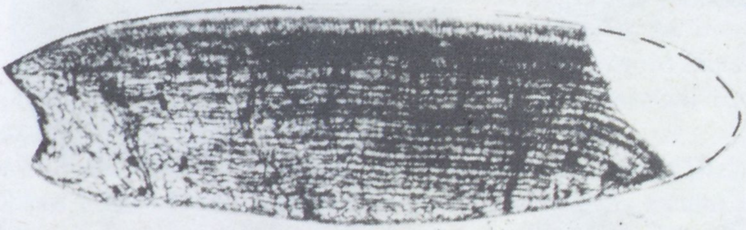

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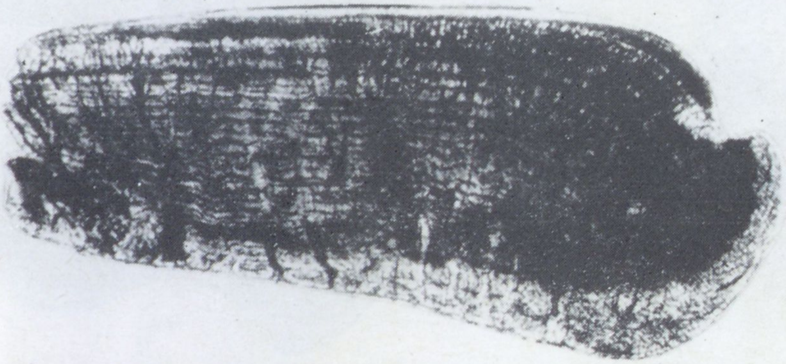

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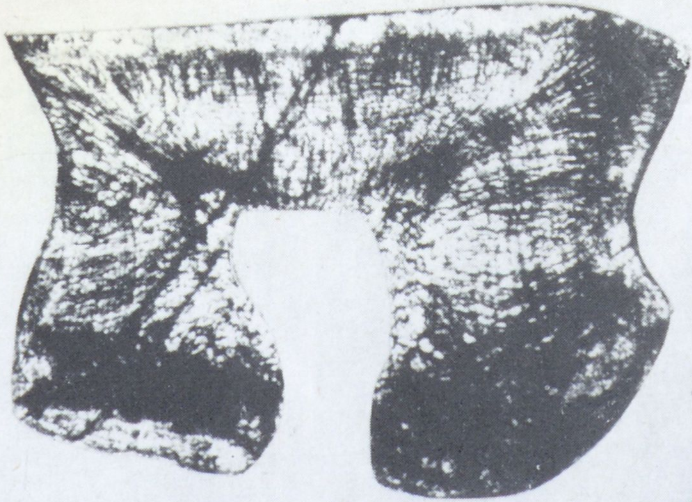
Plate II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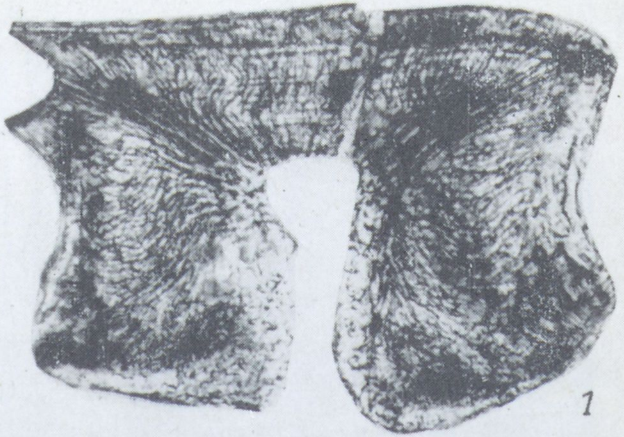
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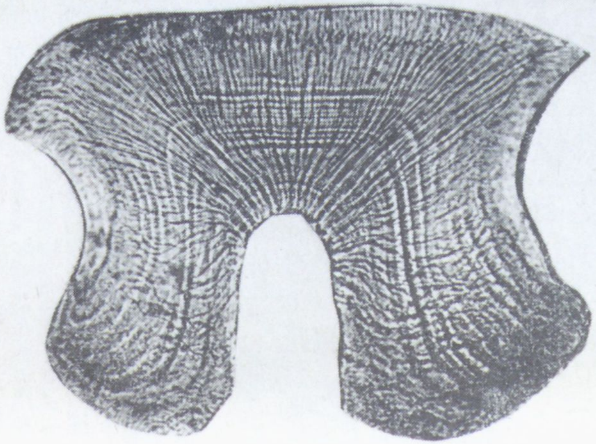
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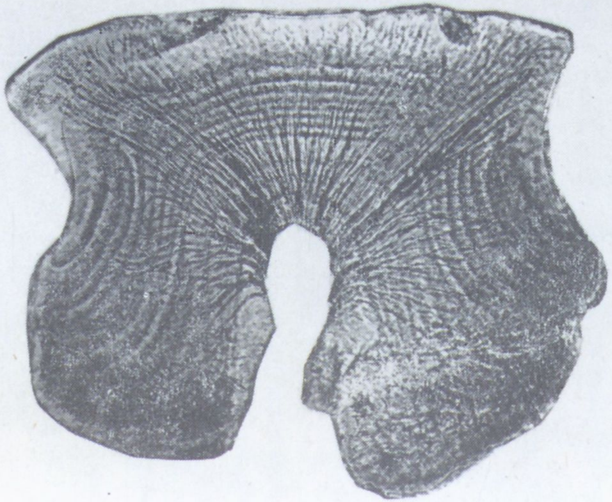
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Possible environmental influences on the morphology of fossil vertebrate scales

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At one single locality, Möllbos 1, in the late Homerian Halla Beds on Gotland the morphologies of some types of the scales of *Thelodus schmidti* differ from normal in that both cephalo- pectoral and postpectoral scales have developed spines. The palaeoenvironment here has previously been interpreted as a possible lagoon, and earlier findings from the invertebrate fauna suggest an extremely muddy habitat.

A comparison of Early Silurian spiny and non-spiny loganellid species indicates that spiny scales were valuable for those vertebrates that lived in muddy habitats; spiny scales are common in the squamation of *Loganellia martinssoni*, which is most abundant in calcareous mudstones and argillaceous limestones; only non-spiny scales occur in another species which is most abundant in pure crinoidal limestones.

On the basis of that, the morphological changes observed in *Thelodus schmidti* at Möllbos 1 have been interpreted as possibly caused by natural selection in a population under severe environmental pressure.

Heterostracans: their ecology, internal structure and ontogeny

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Abstract. The faunal assemblage occurring in the Lower Devonian rocks (Kureika Formation) in the NW part of the Siberian Platform, comprises various groups of vertebrates, invertebrates and plants. Heterostracans are represented by amphiaspids, mostly benthic forms. Ethologically amphiaspids are quite comparable with tadpoles of modern frogs at the early stage of their metamorphosis. In the Kureika biocenosis amphiaspids seem to have been secondary consumers with respect to some invertebrates (ostracodes, soft-bodied mud-eaters) and several free-swimming larvae. At the same time, the amphiaspids, particularly their juveniles served as a usual prey for crossopterygians and arthrodires.

The reconstruction of the internal organs of heterostracans (cranial nerves etc.) by means of marker structures is present. In the structure of the olfactory apparatus and telencephalon, heteroctracans are similar to archaic gnathostomes, considerably differing from osteostracans and lampreys. The type of ontogeny of fossil groups can be established by their definitive morphology. Morphology of heterostracans and osteostracans shows that the gnathostomic and cyclostomic types of ontogeny were realized already in the Palaeozoic, i.e. both types of ontogeny remained somewhat conservative during the whole vertebrate evolution. This allows to consider the type of ontogeny as the main criterion for assignment of separate groups of agnathans to one of the main trends of vertebrate divergence.

Taking into account an extremely attractive motto of the colloquium "Fossil Fishes As Living Animals", it was rather difficult to choose only one trend of research for the paper. Faced with this task, the author preferred a compromise decision, joining the analysis of ecology of heterostracans (amphiaspids) with the analysis of their internal morphology. For several reasons special attention was paid to the internal structure of heterostracans, namely: (1) the information concerning their internal structure enables to consider agnathans as living organisms and not as swimming casts the filling of which is not clear; (2) the internal morphology includes precisely those characters which can serve as fundamental criteria for the assignment of different groups of agnathans to one of the main directions in the evolution of ancient vertebrates.

Ecological characterization of heterostracans (Early Devonian biocenosis in the north-west of the Siberian Platform)

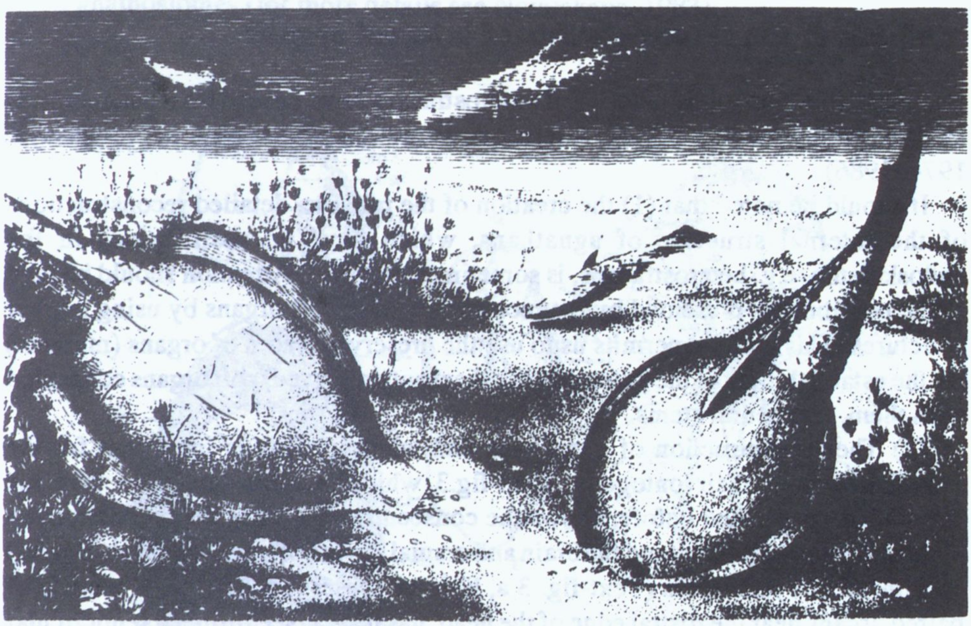
The habitat of amphiaspids (Heterostraci) and their biocenotic relations were studied by us on the example of the Kureika locality material collected by V.V. Menner, Y.M. Eglon and the author of this paper. The locality is situated 80 km from the mouth of the Kureika River, one of the northern right tributaries of the Yenisei River. There we have the lower half of the variegated part of the Kureika Formation exposed. The age of the locality is Early Devonian, Siegenian. A section up to 10 m thick comprises of reddish-brown argillites with interbeds of grey carbonate argillites and argillaceous limestones. There are also interbeds of bone breccia consisting of vertebrate remains. Well-preserved shields of amphiaspids (with undestroyed protruding elements, e.g. lateral edge, mouth tube) were found in the argillites interbedded with bone breccia. Orientation in the position of the shields was not noted. Its absence as well as well-preserved thin parts of the shields witness the death and burial of animals in their habitat. Basing on autochthony of the remains, it is possible to reconstruct the specific biocenotic conditions in the Kureika basin.

According to the data of Matukhin and Menner (1974), the Kureika basin was extremely shallow, containing numerous clay-banks subjected to intensive accumulation of terrigenous, mainly clayey material. The salt regime of the basin during the period considered became almost marine or freshwater-marine under the influence of the transgression from Taimyr. Those conditions turned out favourable for a diverse biocenosis, comprising agnathans (amphiaspids), fishes such as crossopterygians (*Porolepis*), acanthodians (*Onchus* sp.) and arthrodires, and numerous invertebrates and plants. Invertebrates include ostracodes, lingulids and eurypterids, which are rather frequent; gastropods, traces of non-skeletal silt-eaters and charophytes have also been recorded (Matukhin and Menner, 1974).

There occurred various amphiaspids, mainly represented by medium- sized forms: *Angaraspis urvantzevi* Obr., *Siberiaspis plana* Obr., *Olbiaspis coalescens* Obr., *O. latissima* Nov., *Lecaniaspis lata* Nov. and *Argyriaspis tcherkesovae* Nov. (see Novitskaya, 1986). The length of shields ranged from 10 to 18 cm.

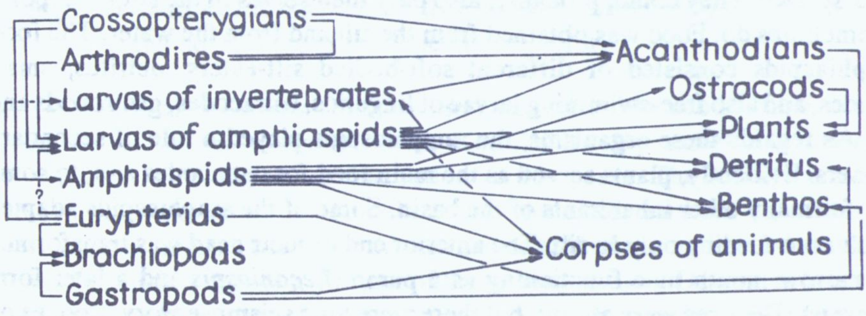
The full length of the biggest mentioned amphiaspid, including the tail part, could be 36-40 cm. The analysis of the general form of the shields and testing of the models of *Olbiaspis coalescens* and *Eglonaspis rostrata* showed that amphiaspids (as well as, evidently, cyathaspids and pteraspids) could easily rise from the bottom and then land smoothly (Aleev and Novitskaya, 1983). In the recent fauna the ethological analogues of amphiaspids could be frog tadpoles at the stage of metamorphosis preceding the appearance of extremities. It seems that in the behavior of heterostracans with thin shields, i.e. amphiaspids, cyathaspids and pteraspids, short states of movement and immobility were alternating.

Judging by the shield construction, amphiaspids, like tadpoles, rather actively covered small distances over the bottom and rose for a short time into the water and up to its surface. They could, probably, also bury themselves in the silt as tadpoles do it sometimes do. Food was obtained from the silt and from the water. The food of amphiaspids consisted of different soft-bodied silt-eaters, detritus, small ostracodes, and also free-swimming larvae of lingulids, ostracodes, gastropods and plants. As regards these organisms, the amphiaspids played a role of secondary consumers. Evidently, plants served as the main food for ostracodes and, to some extent, for many other inhabitants of the basin. Some of the amphiaspids adapted themselves to feeding only in silt. The anterior end of their head was transformed into a narrow mouth tube functioning as a pump (*Lecaniaspis* and a later form *Eglonaspis*). The eyes were absent, but there were long seismosensory grooves on the tube, providing orientation. The reconstructions of some amphiaspids, including *Lecaniaspis*, are given in Text-fig.1.



Text-fig. 1. Reconstruction of amphiaspids in the Kureika basin. In the foreground: *Lecaniaspis lata* Nov. (on the left) and *Olbiaspis coalescens* Obr. (on the right).

In the considered biocenosis the amphiaspids could have become, undoubtedly, an easy prey for crossopterygians (*Porolepis*) -- on the shields of some taimyrian amphiaspids some real traces of healed bites have been found (Novitskaya, 1971). A part of amphiaspids, mainly young individuals, was, probably, exterminated by arthrodires. Several juveniles (at the early shieldless stages) could have become a prey of acanthodians. The supposed food relations in the Kureika basin are given in Text- fig. 2.



Text-fig. 2. Supposed food relations in the Kureika basin.

Methods of the reconstruction of internal organs

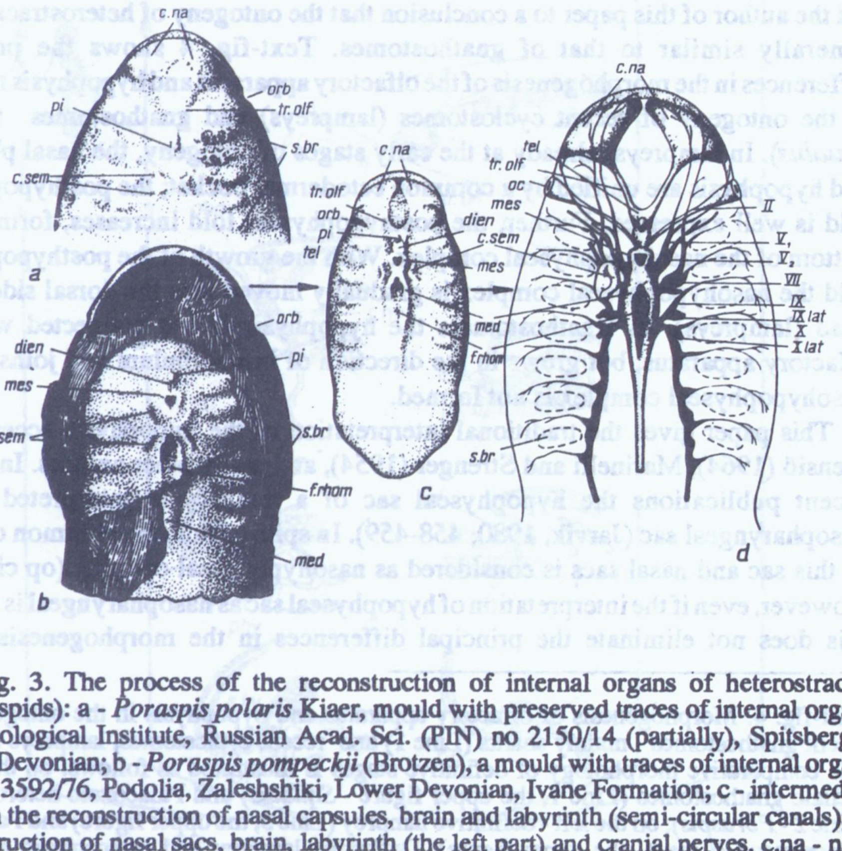
The reconstruction of the exterior of heterostracans have caused less disagreement than the reconstruction of their internal structure (see discussion in Novitskaya, 1974, 1986).

It should be noted that (1) the creation of the reliable, detailed reconstructions of the internal structure of agnathans, which have no ossifications in the endoskeleton, e.g. heterostracans, is sometimes doubtful. Attention should be paid to the possibilities presented by the reconstruction of soft organs by using marker structures. This method permits us to use the preserved traces of organs (markers) for the establishment of the extension of other (not preserved) soft organs connected with them, e.g. neural stems.

(2) The reconstruction of nasal sacs and telencephalon is important for the establishment of their ontogeny. Text-fig.3 which is more complete than the illustrations published before, shows the consecutive stages in the reconstruction of the olfactory apparatus and the brain and cranial nerves of heterostracans. Several specimens of cyathaspids (Text-fig. 3 a, b) have preserved the natural moulds of paired organs near the rostral edge of the head, nasal sacs (see further), semicircular canals, also the pineal organ, diencephalon, mesencephalon, myelencephalon, and gill sacs. The generalized scheme compiled by us shows a mutual position of the organs (Text-fig. 3 c). This scheme can be considered as a marker base enabling to determine the extension of some morphological elements, such as cranial nerves. Their reconstruction is based on the regularities characteristic of vertebrates. Thus, the roots of V, VII, IX, and X nerves enter the lateral wall of myelencephalon. Nerves V and VII pass directly in front of the labyrinth, with nerves IX and X passing behind it. Knowing the position of myelencephalon and semicircular canals in heterostracans, we can mark the initial points of these neural stems. Further, in a vertebrate, the nerves mentioned above innervate the mouth region, orbital region, mandibular and maxillary arches, the supraorbital, infraorbital and other seismosensory canals, the hyoid arch, the first and the following gill arches. The

position of all these organs in heterostracans is known (Text-fig. 3 a-b). Therefore, using them as markers, we can reconstruct the extension of the main branches of nerves V, VII, IX, and X (Text-fig. 3). The length of the other nerves, e.g. opticus (II) and acusticus (VIII), can be established by this method. The scheme (Text-fig. 3 d) obtained in this way shows that the principal features of the central nervous system of heterostracans can be reconstructed rather well. Let us also note that the primitive characters in the structure of other internal organs of heterostracans (labyrinth, gill arches) are quite in conformity with the results of reconstruction: the nervous system of heterostracans corresponds to the archaic level of its organization in the vertebrates.

The pair moulds (or imprints) in the anterior end of the head of heterostracans sometimes have lateral canals (Text-fig. 3). Therefore the traces of the paired anterior structures are considered by us as the traces of nasal sacs of the same kind as in gnathostomes (for more details see Novitskaya, 1983).



Text-fig. 3. The process of the reconstruction of internal organs of heterostracans (cyathaspids): a - *Poraspis polaris* Kiaer, mould with preserved traces of internal organs, Paleontological Institute, Russian Acad. Sci. (PIN) no 2150/14 (partially), Spitsbergen, Lower Devonian; b - *Poraspis pompeckji* (Brotzen), a mould with traces of internal organs, PIN no 3592/76, Podolia, Zaleshshiki, Lower Devonian, Ivane Formation; c - intermediate stage in the reconstruction of nasal capsules, brain and labyrinth (semi-circular canals); d - reconstruction of nasal sacs, brain, labyrinth (the left part) and cranial nerves. c.na - nasal capsules, c.sem - semicircular canals, dien - diencephalon, f.rhom - rhomboidal fossa, mes - mesencephalon, med - myelencephalon, oc - ocular, tr.olf - olfactory tracts, pi - pineal organ, s.br - position of branchial sacs, tel - telencephalon, II - optic nerve, V_1, V_2 - n.trigeminus, VII - branches of VII nerve, IX, IX lat - n.glossopharyngeus, X, X lat - n.vagus (for more details see Novitskaya, 1983).

The space between the nasal sacs and diencephalon considerably exceeds the real size of the telencephalon without olfactory tracts (Text-fig. 3). For that reason, the telencephalon of heterostracans should have olfactory tracts similar to those in archaic gnathostomes (Arthrodira, Elasmobranchii). The traces of the olfactory tracts can be very clearly seen in many specimens of cyathaspids (Text-fig.3a; see also Plates in Novitskaya, 1983).

From the aforesaid we may conclude that the structure of the olfactory apparatus and telencephalon is quite similar in heterostracans and archaic Gnathostomata. The structure of the olfactory apparatus is the main feature distinguishing gnathostomes from cyclostomes (for more details see the paragraph on ontogeny). Therefore, the morphology of heterostracans generally resembles that of Gnathostomata.

On the ontogeny of agnathans

The similarity of the olfactory apparatus of heterostracans and gnathostomes has led the author of this paper to a conclusion that the ontogeny of heterostracans was generally similar to that of gnathostomes. Text-fig. 4 shows the principal differences in the morphogenesis of the olfactory apparatus and hypophysis realized in the ontogeny of recent cyclostomes (lampreys) and gnathostomes (mainly *Squalus*). In lampreys, already at the early stages of ontogeny, the nasal placodes and hypophysis are unified by a common ectodermal pocket; the posthypophyseal fold is well expressed. Further, the posthypophyseal fold increases, forming the bottom of the nasohypophyseal complex. With the growth of the posthypophyseal fold the nasohypophyseal complex is gradually moved into the dorsal side of the head (lampreys). In Gnathostomata the hypophysis is not connected with the olfactory apparatus, but grows in the direction of infundibulum and joins it. The nasohypophyseal complex is not formed.

This paper gives the traditional interpretation of the hypophysis accepted by Stensiö (1964), Marinelli and Strenger (1954), and many other authors. In certain recent publications the hypophyseal sac of a lamprey is interpreted as the nasopharyngeal sac (Jarvik, 1980; 458-459). In spite of this, the common opening of this sac and nasal sacs is considered as nasohypopyseal opening (op cit: 458). However, even if the interpretation of hypophyseal sac as nasopharyngeal is correct, this does not eliminate the principal differences in the morphogenesis of the

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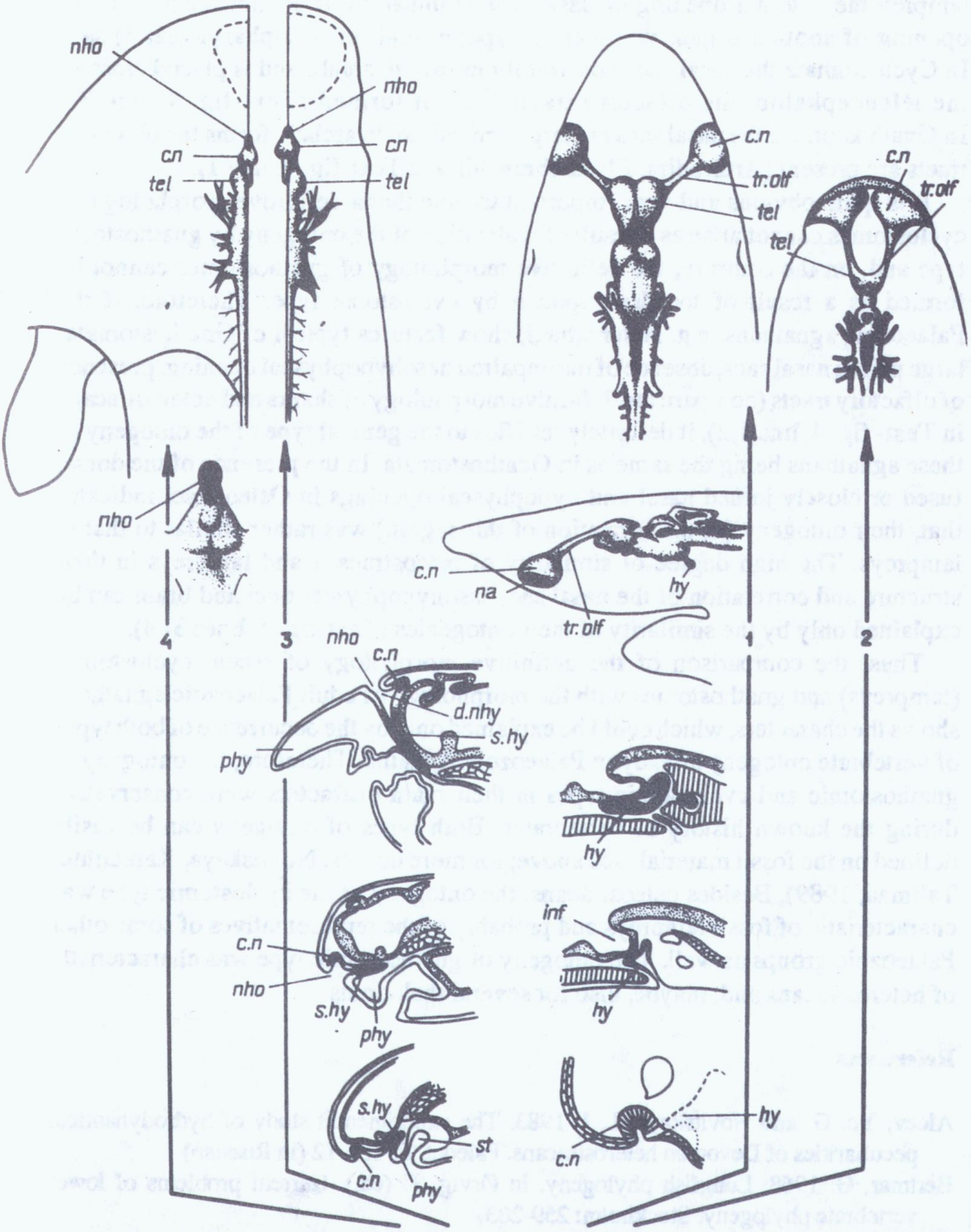
Text-fig. 4. Morphogenesis of olfactory apparatus and hypophysis in the ontogenesis of recent gnathostomes - mainly sharks (Line 1) and recent cyclostomes, lampreys (Line 3). The comparative morphology of definitive stages is illustrated as follows: on the right - archaic gnathostomes (Line 1, the upper figure - *Squalus*) and Palaeozoic heterostracans (Line 2 - *Poraspis*); on the left - definitive lamprey (Line 3, the upper figure) and Palaeozoic osteostracan (Line 4, the upper figure). Definitive lamprey and osteostracan are given according to Janvier (from Jarvik, 1980), the primary stage of ontogeny in gnathostome (Line 1) according to Bertmar, 1968. c.n - nasal sac (or placode), d.nhy - nasohypophyseal duct, hy - hypophysis, inf - infundulum, na - nostril, nho - nasohypophyseal opening, phy - posthypophyseal fold, s.hy - hypophyseal sac, st - stomodaeum, tel - telencephalon, tr.olf - tracti olfactorii.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olfactory organ of lampreys and archaic gnathostomes. In the latter the nasal sacs open into separate nostrils which are not connected with any other organ. In the lamprey the external opening of nasal sacs is unpaired. It is connected with the opening of another organ, viz. that of hypophyseal (or nasopharyngeal ?) sac. In Cyclostomata the nasal sac is outwardly unpaired, small, and is placed close to the telencephalon, the olfactory tracts are not formed (Text-fig. 4, line 3). In Gnathostomata the nasal sacs are large and paired. In archaic forms the olfactory tracts are present (Arthrodira, Elasmobranchii; see Text-fig. 4, line 1).

It is quite obvious and very important to note that a definitive morphology of cyclostomes cannot arise as a result of realization of the ontogeny by gnathostome type and, on the contrary, the definitive morphology of gnathostomes cannot be formed as a result of the development by cyclostome type. Therefore, if the Palaeozoic agnathans, e.g. Heterostraci, show features typical of Gnathostomata: large paired nasal sacs, absence of the unpaired nasohypophyseal opening, presence of olfactory tracts (compare the definitive morphology of sharks and heterostracans in Text- fig. 4, line 1,2), it definitely testifies to the general type of the ontogeny of these agnathans being the same as in Gnathostomata. In the presence of the dorsal fused or closely joined nasal and hypophyseal openings in Osteostraci indicates that, their ontogeny (in the formation of this region) was rather similar to that in lampreys. The high degree of similarity of osteostracans and lampreys in their structure and correlation of the nasal sac, nasohypophyseal duct and brain can be explained only by the similarity of their ontogenies (Text-fig. 4, lines 3- 4).

Thus, the comparison of the definitive morphology of recent cyclostomes (lampreys) and gnathostomes with the morphology of adult Palaeozoic agnathans shows the characters, which could be explained only by the occurrence of both types of vertebrate ontogeny already in Palaeozoic Agnatha. Therefore, the ontogeny of gnathostomic and cyclostomic types in their main characters were conservative during the known history of vertebrates. Both types of ontogeny can be easily defined on the fossil material (see above; for more details: Novitskaya, Karatajūte-Talimaa, 1989). Besides osteostracans, the ontogeny of the cyclostomic type was characteristic of fossil lampreys and probably of the representatives of some other Palaeozoic groups as well. The ontogeny of gnathostomic type was characteristic of heterostracans and, maybe, also for several thelodonts.

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Some peculiarities of osteostracan ecology

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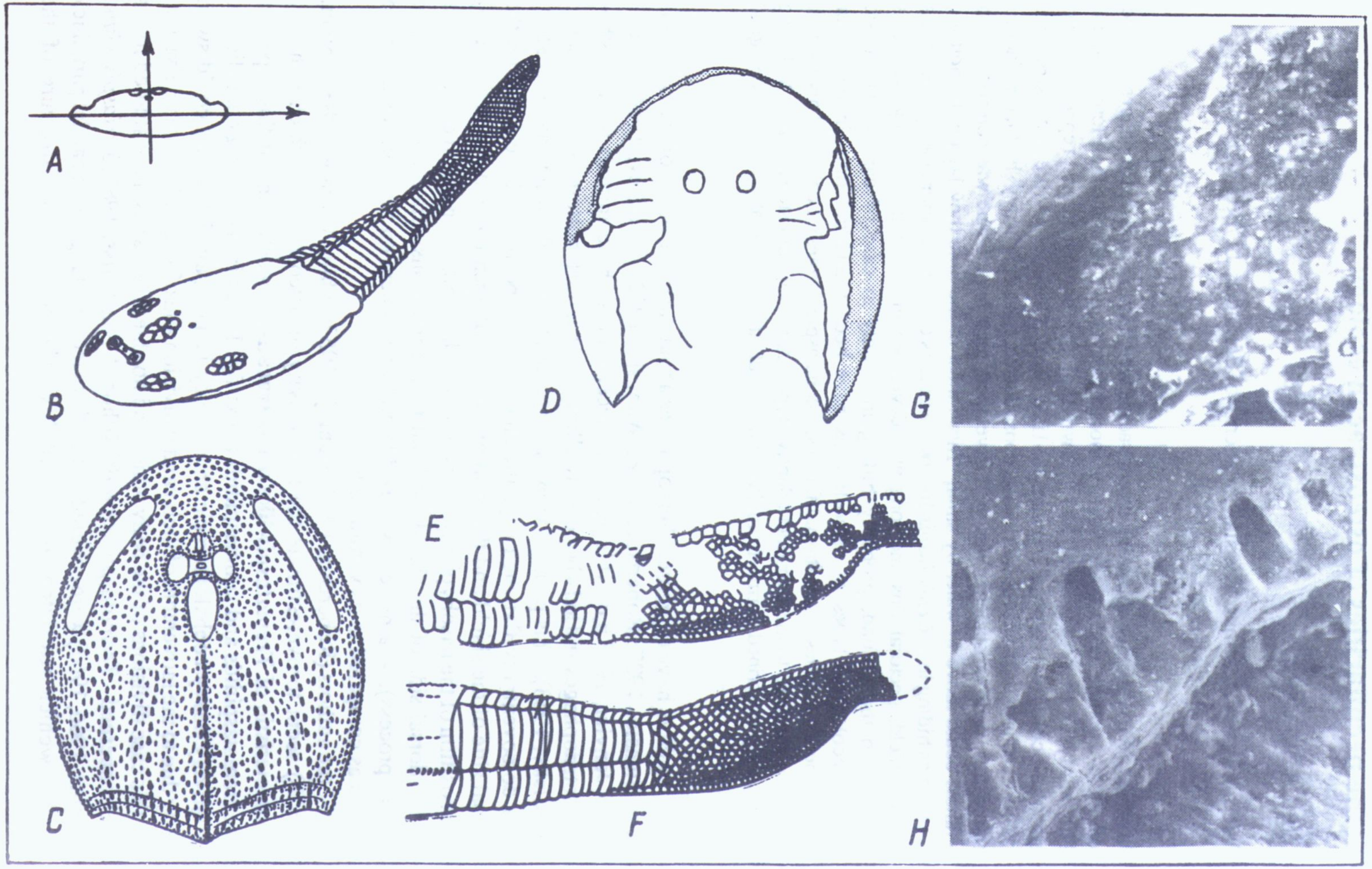
Abstract. We no longer doubt that osteostracans were bentho- and detritophages adapted to bottom-dwelling mode of life. Some authors, however, overestimate their low mobility. The analysis of recent data has shown that the osteostracans represent two morpho-ecological types: *Tremataspis*-like and *Cephalaspis*-like osteostracans. Osteostracans of the first type had a long, consolidated, relatively heavy shield, they lacked paired fins, their exoskeleton was well developed, their bone tissue was compact. Such animals could move in water by small "flits": most of the time they lay on the bottom, sometimes hiding in it. *Cephalaspis*-like osteostracans could move more easily; they had a lighter shield, pectoral fins and long well-developed muscular trunk. They were less attached to the ground, probably hiding in it only in case of danger. The basic morpho-ecological types of osteostracans have been found not only in the major phylogenetic branches (Tremataspidiformes, Cephalaspidiformes). Ecological diversity of the is not confined to these distinct adaptive types. A number of osteostracans, including the recently described forms from Podolia, are of an intermediate morpho-ecological character.

Many authors have expressed their opinions about the mode of life of osteostracans (e.g. Stensiö, 1927; Robertson, 1938; Wängsjö, 1952; Obruchev, 1964; Heintz, 1966; Janvier, 1985 b,c). It is generally accepted that these animals were bentho- and detritophages and led a bottom-dwelling mode of life ("bottom- dwelling" sensu Nikolsky, 1963). This point of view is supported by the following characteristics: 1) a dorsoventrally flattened cephalic shield; 2) the position of the orbits on the dorsal side of the shield and the position of the oral opening on its ventral side; 3) the position of the nasohypophysal opening and the orbits on the most elevated area of the dorsal side of the shield (without taking into consideration the developed spinal process); 4) a more developed lateral line system on the dorsal side of the shield as compared to its ventral side.

Some authors (Robertson, 1938; Wängsjö, 1952; White, Toombs, 1983; Janvier, 1985b) seem to overestimate the low activity of osteostracans, which is highly characteristic of ***Tremataspis*-like osteostracans.** Osteostracans of this type, i.e. the tremataspidids and tannuaspidids (Text-fig. 1) had in fact a long consolidated relatively heavy cephalothoracic shield, they lacked paired fins and could swim only due to the movement of their caudal division and of a part of the trunk division. In this case divisions of the body which had no shield (as far as these studied forms are concerned - *Tremataspis schmidti* Rohon, 1892; Märss, 1986; *Tyriaspis whitei* Heintz, 1966, 1967) were covered by tightly placed, rectangular in caudal part, thick scales wchich restricted their flexibility. The study of the structure of the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exoskeleton of some *Trematapis*-like forms (*Trematapis*, *Dartmuthia*, *Saaremaaspis*; see Stensiö, 1927,1932; Denison, 1951; by means of the SEM: Gross, 1968; Afanassieva, 1986) revealed its conciderable thickness as compared to the length of the shield, a good development of all the layers of the exoskeleton (*Trematapis*, *Dartmuthia*), and a high density of the bony tissues (the genera mentioned above and *Saaremaaspis*). So, the body of these animals had a relatively large specific gravity.

It should be pointed out that the caudal fin of *Trematapis schmidti* differs from a typically epicercal fin of other osteostracans (Janvier, 1985a); its structure slightly resembles a rudimentary epicercal fin. Such relatively well protected osteostracans (Text-fig.2) could move on by "flits" like the heterostracans (Aleev and Novitskaya, 1983), and for most of the time they lay on the bottom, sometimes hiding themselves in its upper layers. The smooth enamel surface of the shield (*Trematapis*, the ventral side of the shield of *Dartmuthia*) or flat rounded tubercles (*Saaremaaspis*, dorsal side of the shield of *Dartmuthia*) and small longitudinal ridges (*Timanaspis*) were no obstacles for them while hiding in the bottom-mud.

Unlike them, ***Cephalaspis*-like osteostracans** (Text-fig.3) with paired fins seem to have been better swimmers and led a more active life. This viewpoint is supported by: 1) improved hydrodynamical characteristics of their shield — it is short, light, triangular, or semicircular with a flat ventral side (*Cephalaspis*, *Mimetaspis*, *Thyestes*, *Procephalaspis*, and others), 2) well developed muscles of the long flexible trunk covered by narrow scales (*Cephalaspis lyelli* Agassiz, 1835), and 3) a typical epicercal caudal fin (*Hemicyclaspis*). A flat ventral side of the shield, its widened lateral parts, cornua (particularly well developed in *Benneviaspis* and *Parameteoraspis*) presented griding planes, providing utmost displacement during the gliding phase of the "flit". The flat shield with sharp edges (sometimes with a rostral angle, a lobe or rostrum) had a small frontal resistance. Pectoral fins did not seem to play the main role in the movement of the body. If we look at a section of the shield in the site of the pectoral fin, we can see that this fin is a continuation of the profile of the lateral part of the shield. While moving up and down, the pectoral fin could considerably change the curvature of the profile and, consequently the lift-force of the right or left "wing" of the shield. So, pectoral fins of osteostracans functioned as ailerons of an airplane, i.e. they served for turning the body around the longitudinal axis, as well as could lift or lower the animal's body during its movement in one direction. The body could turn to the right or to the left by the

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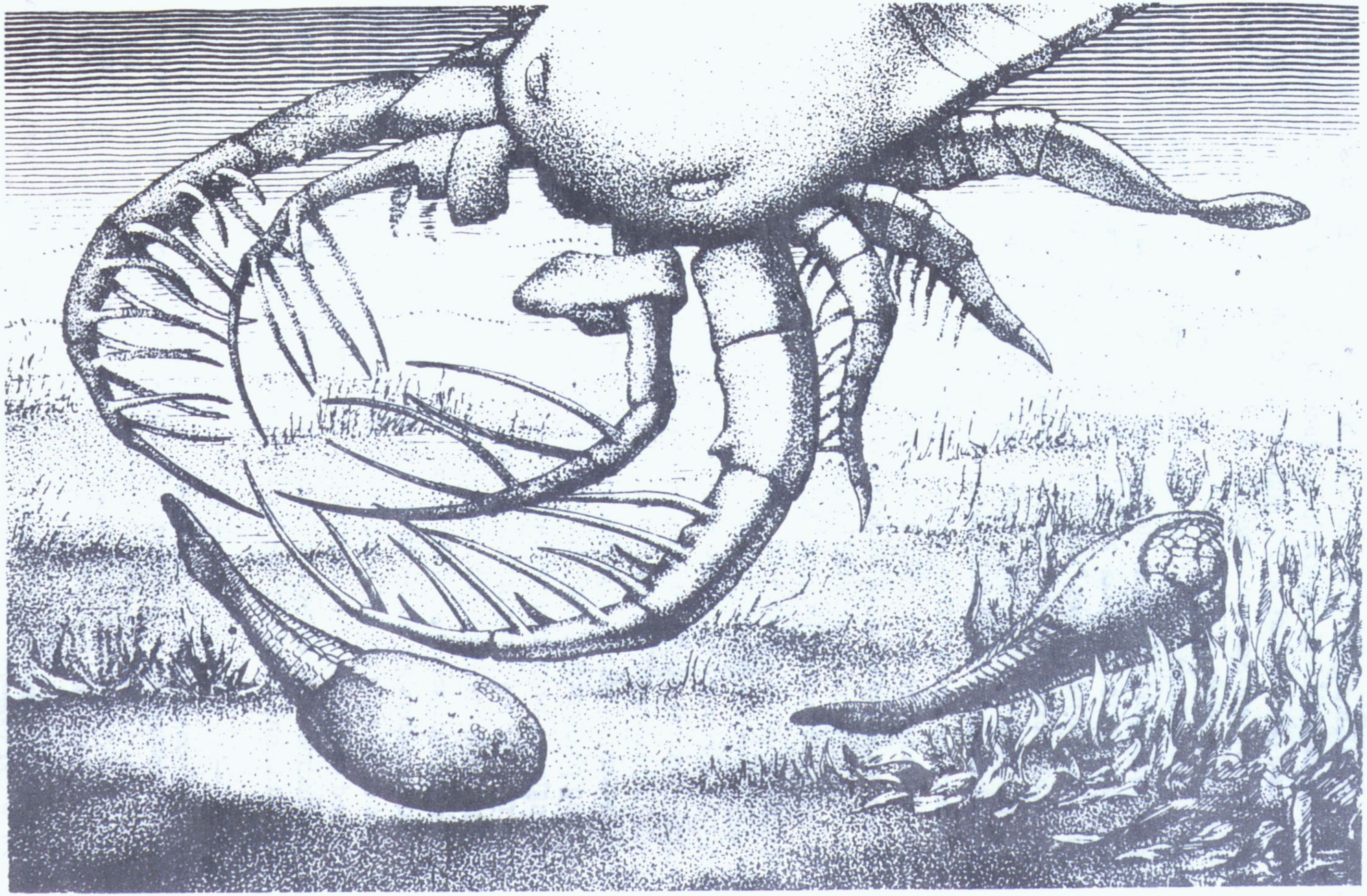
Text-fig.1. *Trematapis*-like osteostracans: A - diagrammatical transverse section of the shield of *Trematapis* through the orbits, B - diagrammatical reconstruction of the body of *Tremaspis* sp., C - *Dartmuthia gemmifera* Patten, dorsal side of the shield (x), D - *Tannuaspis levenkoi* Obr., diagrammatical reconstruction of the shield (from Afanassieva and Janvier, 1985), E - *Trematapis schmidti* Rohon, squamation of the posterior part of the body (x 1.9), F - reconstruction (x 1.5) (E, F - from Märss, 1986), G - *Dartmuthia gemmifera*, broken surface of the dorsal tubercle with the opening of dentinal tubules (SEM, x 500), H - *D. gemmifera*, radiating canals of the middle layer and laminae of isopedin (SEM, x 220) (G, H - PIN N 3256/520, Saaremaa Island, Ludlow, Paadla Regional Stage).



winding the caudal fin horizontally. It seems that the osteostracans of the *Cephalaspis*-like type were not so well adapted to the bottom-dwelling and, perhaps, disguised themselves in the upper layer of the bottom only while fleeing from danger (probably after a leap from the predator). The study of the exoskeleton structure of *Thyestes verrucosus*. Eichwald, 1854 and *Witaaspis schrenkii* (Pander), 1856 (Denison, 1951; Afanassieva, 1985, 1986) showed its relatively small thickness, a weak development of its superficial and basal layers, a high friability of the bony tissue of the middle layer in the exoskeleton. Such a structure of the shield also testifies to active fleeing in case of danger, because such a shield could not protect osteostracans from the "gigantostracans" and predatory fish. The sculpture of the shield of the osteostracans of this type is characterized by small tubercles. Besides such tubercles, *Thyestes verrucosus* had large ones arranged in regular rows. This regular arrangement of the tubercles might testify to an active orientation of the animal's body in the water.

Thus, it is possible to distinguish two basic morpho-ecological types of the osteostracans: *Tremataspis*-like and *Cephalaspis*-like types which were found not only in the major phylogenetic branches (Tremataspidiformes, Cephalaspidiformes), but within the group of Tremataspidiformes (*Tremataspis*, *Thyestes*) as well.

Ecological diversity of osteostracans is not confined to these distinct adaptive types (*Tremataspis*, *Cephalaspis*) only. A number of osteostracans have an intermediate morpho- ecological character, including some forms from Podolia, among them the recently described ones (Text-fig.4). Such osteostracans (the species of the genera *Diademaspis*, *Tegaspis* and others) were of large sizes, had a flat ventral side and a prominent dorsal side of the shield, which was relatively heavy, had well-developed cornua and pectoral fins and, apparently, powerful muscles of the trunk. In other words, a large and relatively heavy shield occurred together with the well-developed trunk and caudal divisions. The study of Podolian material has shown that such forms, rather confined to the bottom, existed together with more active lighter forms. This can be illustrated with the following example. The Ustechko Formation of the Dniestr Series has yielded only a small number of species belonging to the cephalaspidians sensu stricto (Janvier, 1985a) and are typical *Cephalaspis*-like forms: *Mimetaspis glazewskii* Janvier, 1985, *Pattenaspis rogalai* (Balabai), 1962, (Janvier, 1985a; Afanassieva and Voichishin, in press). This formation is characterized by a considerable number of the osteostracans of an intermediate type belonging to the scolenaspidians (Janvier, 1985a), particularly the relatively small *Stensiopelta pustulata*, *Zychaspis siemiradskii* Janvier, 1985, and massive zenaspidids - *Diademaspis stensioei* Afanassieva, 1989, "*Cephalaspis*" *kozlowskii* Zych, 1937, and "*C.*" *podolica* Balabai, 1962. As for the Khmelova Formation overlying the Ustechko Formation, the presence of the osteostracans from the family Benneviaspididae is rather typical. These are

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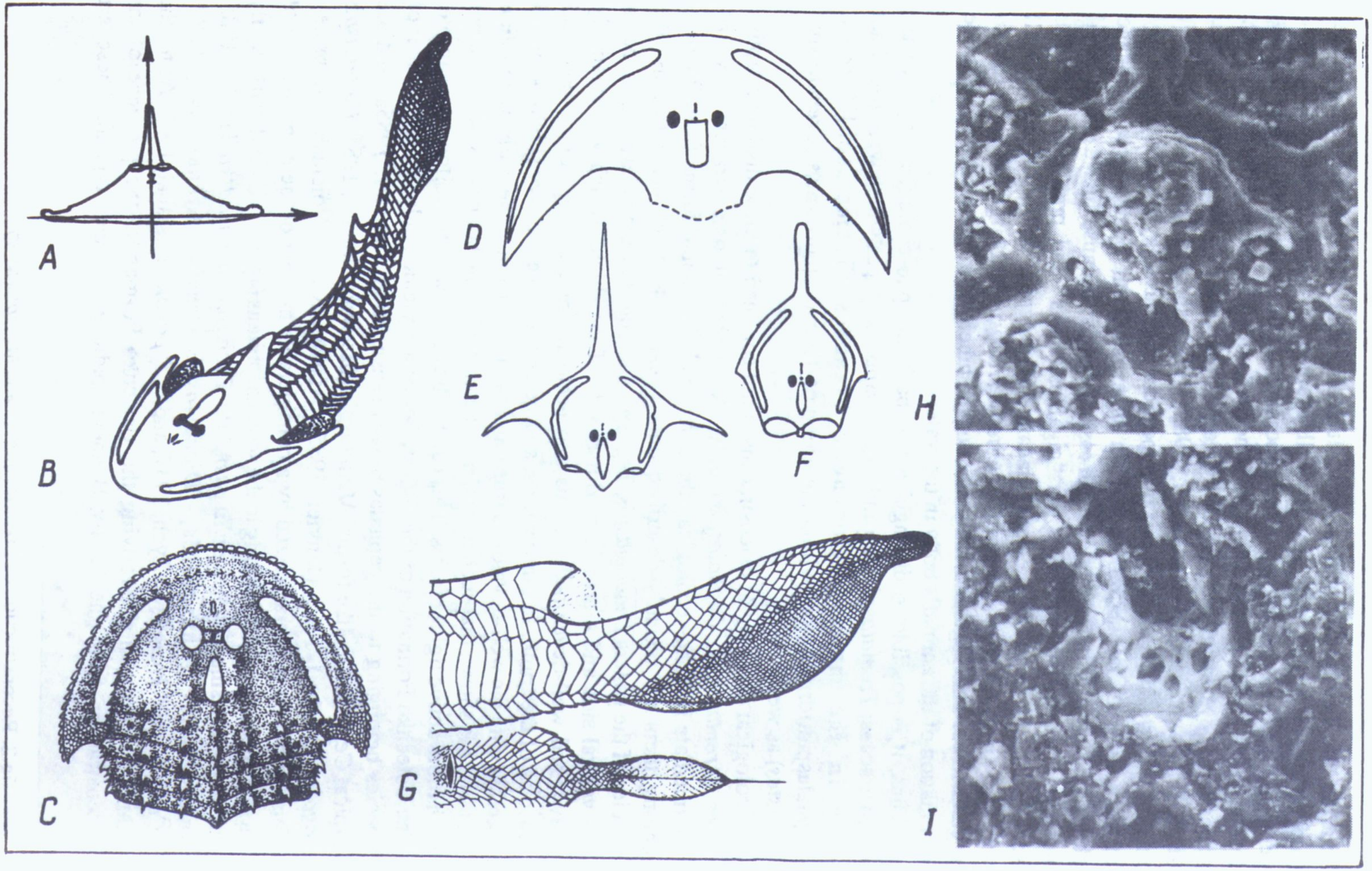
Text-fig.2. Reconstruction of *Tremataspis* sp. and *Mixopterus* sp.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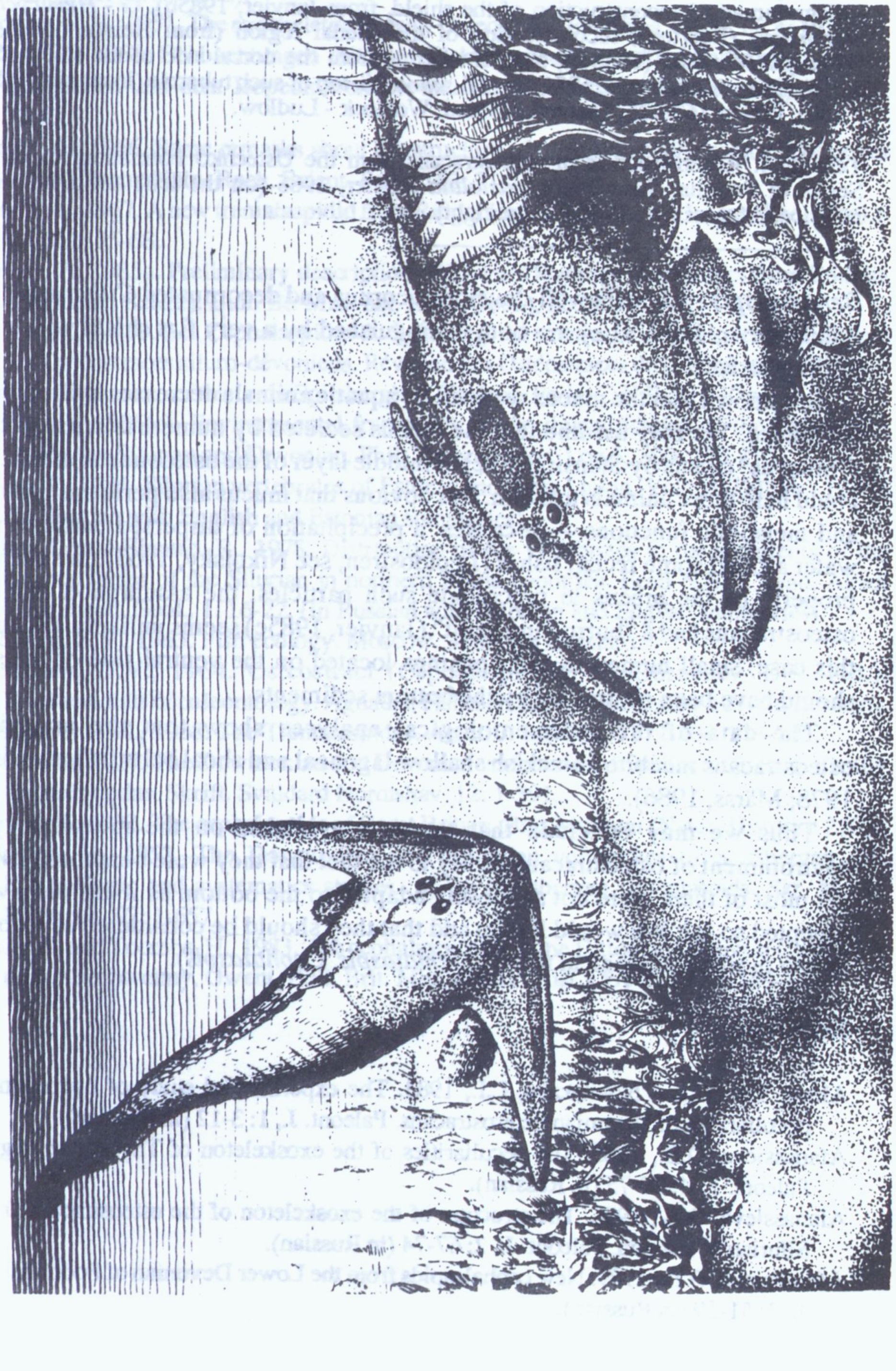

Text-fig.3. *Cephalaspis*-like osteostracans: A - diagrammatical transverse section of the shield of *Cephalaspis* through the orbits, B - diagrammatical reconstruction of the body of "*Cephalaspis*", C - *Thyestes verrucosus* Eichwald, reconstruction of the sculpture of the shield (x 2.8) (from Afanassieva, 1985), D - *Parameteoraspis gigas* (Wängsjö) (x 0.2), E - "*Boreaspis*" *ceratops* Wängsjö, (x 0.7), F - *Spatulaspis costata* (Wängsjö) (x 0.7) (D, E, F - diagrammatical reconstruction of the shield, from Janvier, 1985b), G - *Hemicyclaspis murchisoni* (Egerton), reconstruction of the caudal region (from Heintz, 1966), H - *Witaaspis schrenkii* (Pander), broken tubercle from the dorsal side of the shield (SEM, x 530) (from Afanassieva, 1986), E - *W. schrenkii*, top of such tubercle (inner view) (SEM, x 550), PIN nr 1628/25, Saaremaa Island, Wenlock - Ludlow.

Text-fig.4. Reconstruction of osteostracans from the Ustechko Formation, the Dniestr Series of Podolia: *Stensiopelta pustulata* Janvier, 1985 (on the left) and *Diademaspis stensioei* Afanassieva, 1989 (on the right).

Benneviaspis zychi with well-developed cornua and decornuated *Citharaspis junia* Afanassieva, 1989. They are both distinguished by a very flat shield with a wide gliding surface.

It is known that the mucus secreted by aquatic animals decreases hydrodynamic resistance. We may assume that the mucus secreted by numerous sensory canals ("mucous" canals by Stensiö, 1932) of middle layer of the osteostracan exoskeleton could help these animals to swim. It is obvious that mucus also performs protective and metabolic functions — it causes a precipitation of dispersed particles in the water around some recent fishes (Lepidosiren; see Nikolsky, 1963). In spite of the property of the mucus to precipitate such particles, the assumption that some osteostracans had a "burrowing habit" (Janvier, 1985c) seems unlikely, because, in this case, small numerous gill openings located on the ventral side of the shield should have been obstructed by the bottom sediments.

The data of the sedimentological analyses show that the majority of osteostracans inhabited brackish shallow lagoonal and shoal belts (Märss, Einasto, 1978; Märss, 1986).

Thus we may conclude that the data available on the morphology and enviromment of osteostracans testify to the fact that they were benthonic animals, yet most of them were not so closely adapted to the bottom as it has been widely accepted so far. We would like to add that they should be considered as belonging to two morpho-ecological types (*Tremataspis*, *Cephalaspis*).

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The palaeoecology and evolutionary history of the porolepiform sarcopterygians

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Abstract. The porolepiform fishes were predators, as shown by specimens containing partially swallowed prey fishes. The postcranial morphology of porolepiforms is typical of 'unsteady' swimmers (sensu Webb, 1982), and probably allowed both rapid acceleration and tight turning. A very similar morphology is seen in certain early lungfishes. The holoptychiid postcranial morphology seems to have remained unchanged throughout the Middle and Upper Devonian, and the porolepiforms are on the whole a morphologically very conservative group; the reason for this conservatism is uncertain. When two porolepiform taxa occur at the same locality, they normally differ greatly in size. Porolepid porolepiforms are known from both marine and alluvial sediments, but holoptychiids are absent in fully marine deposits. During the Middle Devonian, porolepiforms are often the largest predators in the faunas where they occur, but in the Upper Devonian this role is taken over by very large eusthenopterid osteolepiforms.

Introduction

This paper aims to provide a brief overview of the palaeobiology of the Devonian fish group Porolepiformes (Osteichthyes, Sarcopterygii). Two areas will be considered in detail; one is porolepiform autecology, the other is the diversity patterns and faunal associations of the group, and the way these changed during the course of the Devonian.

The Porolepiformes are a group of lobe-finned bony fishes (Osteichthyes, Sarcopterygii), known from the Siegenian to the end of the Devonian (Andrews et al., 1967). The group has traditionally been regarded as an order of the subclass Rhipidistia, class Crossopterygii (see for example Andrews and Westoll, 1970), but recent work indicates that porolepiforms are more closely related to lungfishes than to osteolepiform and rhizodont 'rhipidistians' (Ahlberg, 1989a). Two suborders, the Porolepidae (or Porolepididae) and the Holoptychiidae (Text-figs. 1B, 3A), are recognized within the Porolepiformes (Jarvik, 1942). The Porolepidae, which comprise the genera *Porolepis* and *Heimenia*, are characterized by rhomboid scales and the possession of cosmine. The members of the Holoptychiidae, which include *Holoptychius*, *Glyptolepis* and *Laccognathus* as well as some other genera, all have cycloid scales and lack cosmine. Outgroup comparison shows that the defining characters of the Holoptychiidae are autapomorphic, whereas those of the Porolepidae are primitive for the Porolepiformes. However, even though the group Porolepidae has no taxonomic reality, the members of the group are phenetically uniform. Throughout this paper, the terms 'Porolepidae' and 'porolepids' are used in a non-taxonomic sense to designate taxa with a primitive porolepiform morphology. As might be expected, the earliest known porolepiforms are porolepids; the stratigraphic range of the Porolepidae is Siegenian to Eifelian, that of the Holoptychiidae is Eifelian to Uppermost Devonian (Andrews et al., 1967; Lyarskaya, 1981).

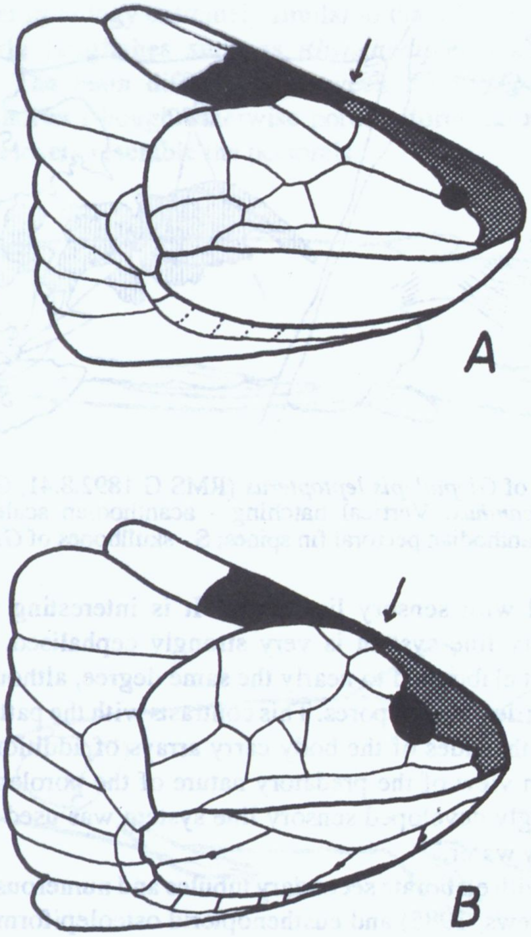
Abbreviations used in the text:

BMNH	- British Museum of Natural History
DCH	- Dartmouth College, Hannover, New Hampshire
MGUH VP	- Geological Museum, University of Copenhagen
MPP	- Musée de Paléontologie, Paris
NMC	- National Museum of Canada, Ottawa
RMS G	- Royal Museum of Scotland, Edinburgh

Functional morphology and autecology

The porolepiforms have skulls of a 'rhipidistian' pattern, with a dentition of conical teeth, amphistylic jaw suspension and a complete intracranial joint. In the serially ground specimen of *Glyptolepis groenlandica* the autopalatine is fused to the ethmosphenoid in three separate places (Jarvik, 1972), which indicates that there was no lateral movement of the palatoquadrate relative to the braincase. The intracranial joint may however have been mobile, as the ventral articulation has the appearance of a functional sliding joint. All known porolepiforms have relatively broad, blunt-nosed heads. The porolepids differ from the holoptychiids in having a longer anterior cranial division (Text-fig. 1), as well as a posteriorly shallow lower jaw. The functional significance of these differences is uncertain.

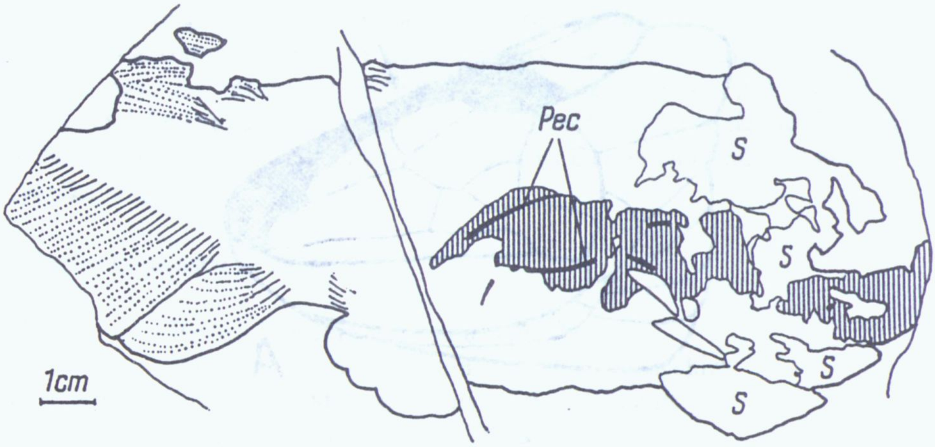
The porolepiform dentition, composed of large fangs and smaller marginal teeth, is unmistakably adapted for catching sizable prey. A characteristic feature is the presence of a parasymphysial toothplate carrying a whorl of small fangs as well as some other teeth (Jarvik, 1972). This toothplate is normally small, but in an undescribed holoptychiid from the Frasnian of Scotland, it seems to have been considerably enlarged (Ahlberg, in press). Additional evidence for a predatory lifestyle comes from two Scottish specimens of *Glyptolepis*, BMNH P60446 (Achanarras, Caithness) and RMS G 1892.8.41 (Gamrie, Banffshire), which died while trying to swallow other fishes. In the Achanarras specimen the prey is a smaller *Glyptolepis* (Trewin, 1986), whereas in the Gamrie fossil it is an acanthodian of the genus *Cheiracanthus* (Text-fig. 2). In both cases the prey item has been swallowed head first to minimize resistance from scales and fin spines, which was probably part of normal hunting behaviour. Both prey fishes are however proportionately very large, and only partly swallowed. Although interesting as direct evidence of porolepiform piscivory, these two specimens are clearly



Text-fig. 1: Skull reconstructions of a porolepid (A) and a holoptychiid (B), showing differences in proportions. Shaded elements - skull roof; arrow - intracranial joint. Modified from Jarvik (1972).

'abnormal' in that the predator did not succeed in swallowing its prey, and it is possible that the prey species represented are not among those normally taken by *Glyptolepis*.

The cephalic sensory canals of porolepiforms always carry branching secondary tubules. In *Porolepis* these are relatively short, and in some individuals the sensory line pores are restricted to narrow bands above the main sensory canals, although single lines of pores (as seen in most primitive osteichthyans) are unknown. In holoptychiids the secondary tubules are usually so strongly developed that all the bones of the skull roof and cheek (except the posterior part of the maxilla) are



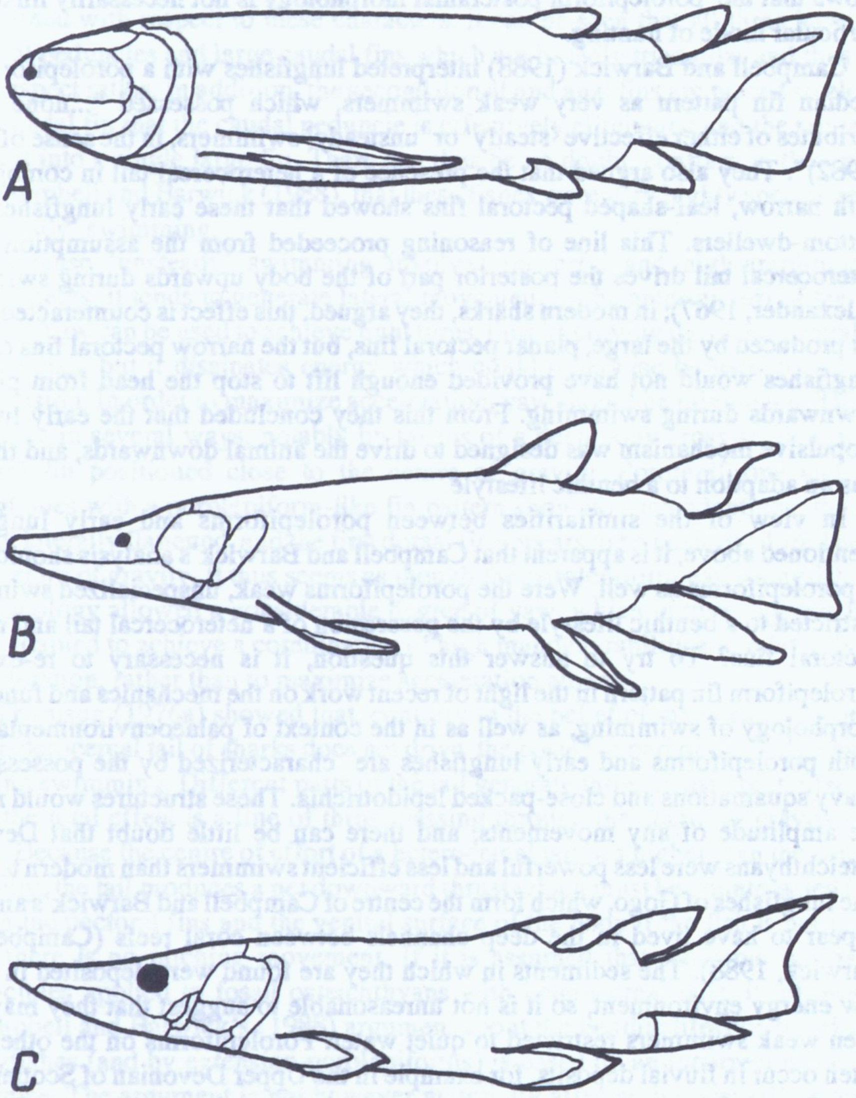
Text-fig 2: Specimen of *Glyptolepis leptopterus* (RMS G 1892.8.41, Gamrie) which has swallowed a *Cheiracanthus*. Vertical hatching - acanthodian scales; dotted lines - lepidotrichia. Pec - acanthodian pectoral fin spines; S - skullbones of *Glyptolepis*.

completely covered with sensory line pores. It is interesting to note that the porolepiform sensory line system is very strongly cephalised. The postcranial sensory lines are not elaborated to nearly the same degree, although each sensory line scale usually carries several pores. This contrasts with the pattern in rhizodonts (see below), where the sides of the body carry arrays of additional sensory lines (Andrews, 1985). In view of the predatory nature of the porolepiforms, it seems likely that the strongly developed sensory line system was used to detect prey in the dark or in murky water.

Sensory canals with elaborate secondary tubules and numerous pores also occur in rhizodonts (Andrews, 1985) and eusthenopterid osteolepiforms (Jarvik, 1944). However, the porolepiforms may have been the first group to evolve this feature; the earliest known porolepiform (*Porolepis*) is Siegenian, whereas the earliest eusthenopterid (*Tristichopterus*) is Givetian. At any rate, until the late Givetian the porolepiforms were the only fishes in their particular communities which possessed such elaborate sensory line systems.

The porolepiform postcranial morphology has only been described for the holoptychiids *Glyptolepis* (Text-fig. 3A) and *Holoptychius*. Both genera have essentially cylindrical bodies, with lateral flattening probably limited to the caudal region. The caudal fin is deeply heterocercal with a small epichordal lobe, and the median fins cluster close to the tail. The pectoral fins are long and leaf-shaped, whereas the pelvic fins are short and round; this morphological disparity between the two sets of paired fins is unique to porolepiforms. Andrews and Westoll (1970) interpreted the porolepiform pectoral fin as very flexible and mobile, but recent work (Ahlberg, 1989a) has shown that the glenoid of the pectoral girdle was narrow and strap-shaped, and pectoral fin mobility accordingly restricted to a modest degree of vertical movement. The lepidotrichial fringes of the pectoral fin may have functioned as 'ripple generators', rather like the long anal fin of gymnotid teleosts.

A postcranial morphology extremely similar to that of porolepiforms occurs in a number of early lungfishes such as *Rhynchodipterus* and *Griphognathus* (Text-fig. 3B,C). The main differences between the two groups are that the lungfishes have shorter (though otherwise porolepiform-like) pectoral fins, and pelvic fins which closely resemble the pectorals.



Text-fig. 3: Holoptychiid and lungfishes showing similar body morphologies. A - *Glyptolepis*; B - *Rhynchodipterus* (modified from Lehman 1966); C - *Griphognathus* (from Campbell and Barwick 1988).

Some authors (Andrews and Westoll, 1970; Trewin, 1986) have suggested that the posteriorly placed median fins of holoptychiid porolepiforms indicate that these fishes were ambush predators. According to this interpretation, the posterior position of the median fins is a specialization for rapid acceleration, that is 'unsteady' swimming in the sense of Webb (1982). However, the fact that a very similar fin pattern is present in a number of presumably non-predatory lungfishes shows that the porolepiform postcranial morphology is not necessarily linked to a particular mode of hunting.

Campbell and Barwick (1988) interpreted lungfishes with a porolepiform-like median fin pattern as very weak swimmers, which possessed "...none of the attributes of either effective 'steady' or 'unsteady' swimmers, in the sense of Webb (1982)". They also argued that the presence of a heterocercal tail in combination with narrow, leaf-shaped pectoral fins showed that these early lungfishes were bottom-dwellers. This line of reasoning proceeded from the assumption that a heterocercal tail drives the posterior part of the body upwards during swimming (Alexander, 1967); in modern sharks, they argued, this effect is counteracted by the lift produced by the large, planar pectoral fins, but the narrow pectoral fins of early lungfishes would not have provided enough lift to stop the head from pitching downwards during swimming. From this they concluded that the early lungfish propulsive mechanism was designed to drive the animal downwards, and that this was an adaption to a benthic lifestyle.

In view of the similarities between porolepiforms and early lungfishes mentioned above, it is apparent that Campbell and Barwick's analysis should apply to porolepiforms as well. Were the porolepiforms weak, unspecialized swimmers, restricted to a benthic lifestyle by the possession of a heterocercal tail and narrow pectoral fins? To try to answer this question, it is necessary to re-examine porolepiform fin pattern in the light of recent work on the mechanics and functional morphology of swimming, as well as in the context of palaeoenvironmental data. Both porolepiforms and early lungfishes are characterized by the possession of heavy squamations and close-packed lepidotrichia. These structures would restrict the amplitude of any movements, and there can be little doubt that Devonian osteichthyans were less powerful and less efficient swimmers than modern teleosts. The lungfishes of Gogo, which form the centre of Campbell and Barwick's analysis, appear to have lived in the deep channels between coral reefs (Campbell and Barwick, 1988). The sediments in which they are found were deposited in a very low energy environment, so it is not unreasonable to suggest that they may have been weak swimmers restricted to quiet water. Porolepiforms on the other hand often occur in fluvial deposits, for example in the Upper Devonian of Scotland and East Greenland, and the same is true for the lungfish *Rhynchodipterus* (Text-fig. 3B). This would seem to put a lower limit on the swimming ability of porolepiforms and *Rhynchodipterus* (if not other early lungfishes), in that they must have been powerful enough to make headway against a modest current.

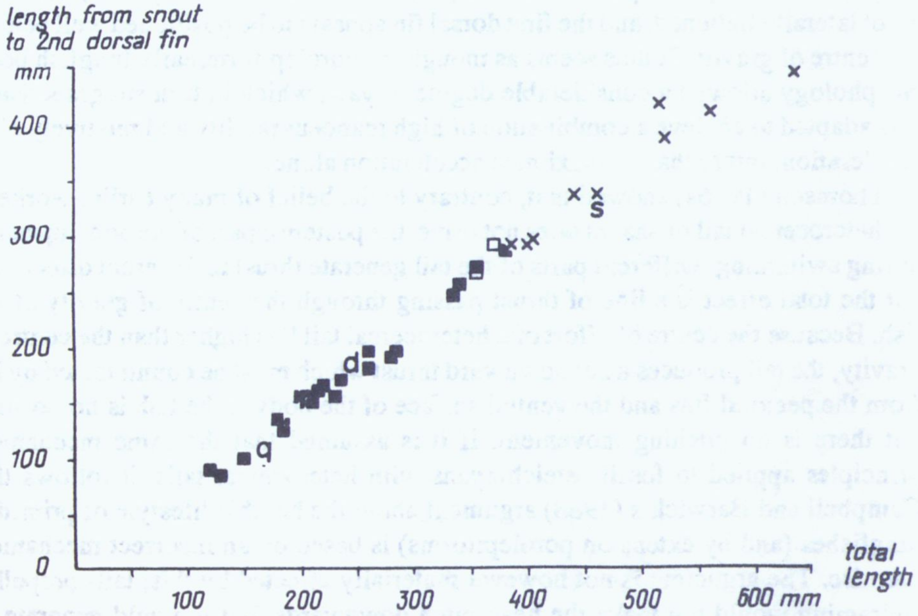
As Webb (1982) pointed out, the ideal body designs for 'steady' (sustained high cruising speed) and 'unsteady' (rapid acceleration) swimming differ in a number of respects beside median fin positions. Thus, a typical 'steady' swimmer such as the mackerel (*Scomber*) has a spindle-shaped body with a narrow caudal peduncle and a caudal fin with a relatively small area but a high aspect ratio. An 'unsteady' swimmer, on the other hand, will have a deep caudal peduncle and a large caudal fin of low aspect ratio. If the *Glyptolepis*, *Rhynchodipterus* and *Griphognathus* are examined with respect to these characters, it can be seen that all three have deep caudal peduncles and large caudal fins which are broadly triangular and thus have low aspect ratios. In addition, the second dorsal and anal fins are placed so close to the caudal fin that the caudal peduncle is effectively eliminated and the tail region turned into a single large fin. There can thus be no doubt, contrary to the opinion of Campbell and Barwick (1988), that these fishes were very highly specialized for 'unsteady' swimming.

Because 'unsteady' swimming involves powerful and high-amplitude tail movements, it tends to generate lateral movement of the anterior part of the body (yaw). Yaw can be used to achieve tight turns, thus improving the manoeuverability of the fish, but it dissipates energy which could otherwise be used for forward propulsion. In order to maximize acceleration, yaw should be minimized. This can be done in several ways, notably by means of a deep body cross-section or by a dorsal fin positioned close to the centre of gravity. Porolepiforms and early lungfishes with a porolepiform-like fin pattern show no such adaptions; the body is not laterally flattened, and the first dorsal fin appears to be positioned well behind the centre of gravity. It thus seems as though the porolepiform/early lungfish body morphology allowed a considerable degree of yaw, which in turn suggests that it was adapted to achieve a combination of high manoeuvrability and relatively high acceleration, rather than to maximize acceleration alone.

Thomson (1976a) showed that, contrary to the belief of many earlier workers, the heterocercal tail of sharks does not drive the posterior part of the body upwards during swimming. Different parts of the tail generate thrust in different directions, but the total effect is a line of thrust passing through the centre of gravity of the fish. Because the centre of effort of a heterocercal tail lies higher than the centre of gravity, the tail produces a net downward thrust which must be counteracted by lift from the pectoral fins and the ventral surface of the body if the fish is not to sink, but there is no pitching movement. If it is assumed that the same mechanical principles applied to fossil osteichthyans with heterocercal tails, it follows that Campbell and Barwick's (1988) argument about the benthic lifestyle of primitive lungfishes (and by extension porolepiforms) is based on an incorrect mechanical premise. The argument is not however materially affected by this; tail- propelled swimming would not make the head pitch downwards, but it would generate an overall downward force which unless counteracted by some source of lift would eventually drive the fish against the substrate.

As can be seen, the resolution of this particular argument hinges on whether the degree of lift produced by the belly and pectoral fins during tail-propelled swimming was great enough to gravity. This is of course unknown, and strictly speaking unknowable, although experiments with models might give some clue to the answer. An important point to consider, however, is the fact that Recent benthic fishes with heterocercal tails, such as *Pristis*, *Orectolobus* and *Cestracion*, all have large pectoral fins and are capable of 'skimming' over the seabed with very fine control of their vertical movements. The obvious conclusion to be drawn from this is that a propulsive system which uncontrollably pushes the animal against the substrate must be disadvantageous for a bottom-dwelling fish. It is not difficult to see why, as such a system would be mechanically inefficient (through friction or snagging on the substrate) and would also entail considerable risk of injury. Far from being evidence of a bottom-dwelling lifestyle, a locomotory apparatus which is adapted to drive the animal downwards is essentially incompatible with such a mode of life.

The skull morphologies and sensory systems of early lungfishes furnish strong independent evidence of a benthic lifestyle (Campbell and Barwick, 1988), which suggests that these forms at least were able to control their vertical movements.



Text-fig. 4: Plot of second dorsal fin position. Black squares - *Glyptolepis leptopterus*; crosses - *G. polysquama*; white squares - *G. groenlandica*; 'q' - *G. quebecensis* (NMC 4328); 's' - Frasnian *Holoptychius* from Scaumenac Bay (DCH 38.71.10672); 'd' - Famennian *Holoptychius* from Dura Den (BMNH P6407).

There is no feature of porolepiform morphology which directly points towards a benthic mode of life, but the same is true for several Recent predatory fishes which typically stay within one or two metres of the substrate (personal observation of *Esox* and *Perca*). It is thus not impossible that the porolepiforms led a 'quasi-benthic' life.

On the whole, the original interpretation of porolepiforms as 'unsteady' swimmers appears to be well founded. It seems most probable that they used paired and median fin undulations for slow swimming, with the caudal fin being used to produce rapid acceleration and sharp turns. Such a locomotory pattern is clearly suitable for an ambush predator, but in the early lungfishes with a porolepiform-like body morphology the same capacity for rapid manoeuvring and acceleration was presumably used as an escape mechanism.

In comparison with Devonian lungfishes and osteolepiforms, the holoptychiid porolepiforms show very little variation with respect to the postcranial morphology (the porolepid body morphology is poorly known). A comparison of fin positions in *Glyptolepis leptopterus* and *G. polysquama* (="*Glyptolepis paucidens*" in part; see below), together with some specimens of *Glyptolepis groenlandica*, *G. quebecensis* and *Holoptychius* (from both Lower Frasnian and Upper Famennian localities), fails to show statistically significant differences between any of the taxa (second dorsal fin, Text-fig. 4; the other fins give similar results). Although most of the samples are small, and several holoptychiid genera are not represented, the analysis still suggests that in certain lineages at least the body morphology and fin pattern remained unchanged from the Eifelian/ Givetian boundary to the end of the Devonian, a period of approximately 35 million years. In most holoptychiids the cranial morphology is equally conservative, though fragments of an aberrant taxon are known from the Frasnian of Scotland (Ahlberg, in press).

Biogeography and environment

Any attempt to understand Devonian fish biogeographics is seriously hampered by the patchy distribution of data. South America and Africa in particular are still largely blank areas. For this reason, it seems unwise and premature to make any detailed statements about porolepiform biogeography. At present the group is known from all the fragments of the 'Old Red Landmass' (sensu Thomson, 1980; Europe, North America, Greenland and Spitzbergen) as well as from Siberia (Obruchev, 1941) and Iran (Blieck et al.,1980). Thomson (1969), following Lehman (1966), claimed that porolepiforms also occur in Antarctica and Australia. The records from these continents are however very questionable. The Antarctic material attributed to *Holoptychius* by Woodward (1917) actually pertains to an osteolepiform (Grande and Eastman, 1986), and the supposed fragments of *Holoptychius* from Australia are either indeterminable (Hills, 1932) or almost certainly not porolepiform (Fergusson et al., 1979). It is possible that porolepiforms were absent from these continents, There is rather more information about the environmental distribution of the porolepiforms. Porolepids occur both in fluviatile (Spitzbergen) and marine (Rhineland) sediments. *Powichthys*, which may be the sistergroup to the Porolepiformes, also comes from marine deposits (Jessen, 1980). Holoptychiids, on the other hand, are largely restricted to non- marine sediments such as the lacustrine strata of the Orcadian basin and Scaumenac Bay, and the fluviatile Old Red Sandstone of Scotland, East Greenland and the Baltic States. Marine rocks containing holoptychiid material are typically marginal in aspect, containing a limited invertebrate fauna and often large fragments of land plants; good examples are the "*cellulosa* marl" of the Baltic region (Gross, 1950), the Upper Devonian sediments of Colorado and Arizona (Denison, 1951) and the Khush- Yeilagh formation of Iran (Blieck et al., 1980). The fully marine Lower Frasnian fish faunas of Bergisch Gladbach (Ørvig, 1960, 1961) and Gogo contain no holoptychiids. This absence is probably significant, for many other elements of these faunas (osteolepiforms, lungfishes, *Coccosteus*-like arthrodires, antiarchs) occur together with holoptychiids in non-marine assemblages. If holoptychiids could tolerate fully marine conditions, they would almost certainly be present in faunas of this type.

To summarize, porolepid porolepiforms are known both from fully marine and non-marine deposits, whereas holoptychiids occur in freshwater and marginal marine (lagoonal/estuarine?) sediments but seem to be absent from fully marine environments. Thomson (1980) suggested that *Holoptychius* may have been anadromous, as it is sometimes found in marine sediments and has a world-wide distribution. However, the evidence for a world-wide distribution is not entirely convincing (see above).

Evolutionary history and faunal associations

In the Lower Devonian of Spitzbergen (Jarvik, 1942, 1972), Poland (Kulczycki, 1960) and the Rhineland (Gross, 1936; Jessen, 1989), primitive porolepiforms assigned to *Porolepis* and *Heimenia* occur as the only osteichthyans in faunas dominated by placoderms and agnathans. The porolepiform specimens vary in size from small to very large; certain individuals such as MPP SVB1 (Spitzbergen; Jarvik 1972, Plate 6, fig.1) probably did not exceed 30 cm in total length, whereas one the of the jaw fragments from the Holy Cross Mountains of Poland figured by Kulczycki ("specimen no. 7"; Kulczycki, 1960, Text-fig. 4, Pl. V A) represents one of the largest known porolepiforms. Unfortunately, the fragmentary nature of the material makes it difficult to determine whether this variation in size reflects the presence of several species at each locality.

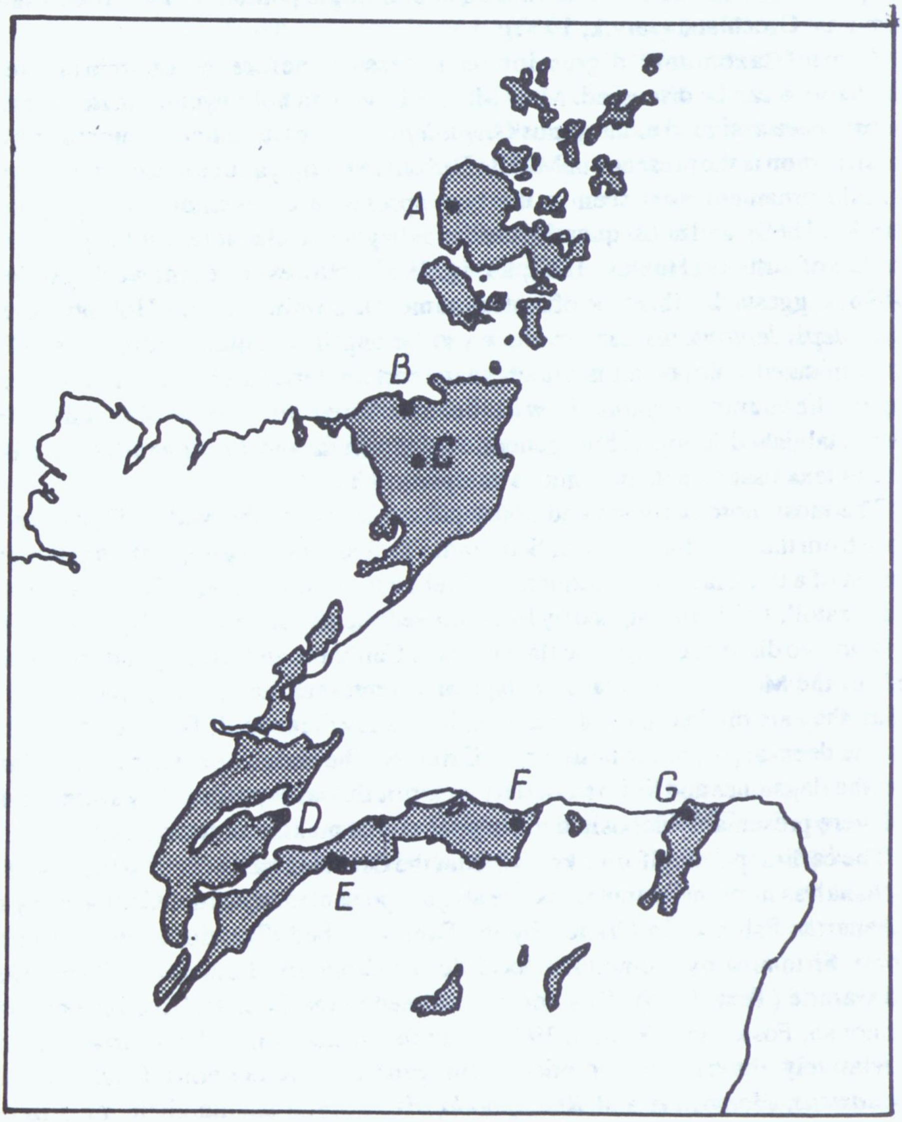
The Middle Devonian porolepiforms are much better known than the Lower Devonian taxa, as numerous articulated specimens have been recovered from Middle Old Red Sandstone localities in Scotland and more recently East Greenland (Jarvik, 1972). Fragmentary but often well-preserved porolepiform material also occurs throughout the Middle Devonian sequence in the Baltic region (Gross, 1950). At the beginning of the Middle Devonian, the first holoptychiids appear, and the porolepids disappear from the fossil record. The replacement seems to have occurred quite rapidly. The earliest known holoptychiids are found in the Baltic lower Eifelian (Pernau=Pärnu Beds), where they occur together with porolepids (Gross, 1950), but by the end of the Eifelian the porolepids have already disappeared (Gross, 1950; Lyarskaya, 1981). In Scotland and East Greenland the earliest Middle Devonian porolepiforms occur near the Eifelian-Givetian boundary, and are all holoptychiids with the possible exception of a single porolepid postparietal shield from East Greenland (Jarvik, 1950).

A brief taxonomic digression is necessary before holoptychiid faunal associations can be discussed. Most Middle Devonian holoptychiid material has in the past been assigned to the genus *Glyptolepis*. The main character supporting this classification is the presence in Middle Devonian holoptychiids of a distinctive type of scale ornament, first seen in the type species of *Glyptolepis*, *G. leptopterus*, (Pander, 1860), and subsequently used as a diagnostic character for the genus by a number of authors (Huxley, 1861; Ørvig, 1957). However, recent work (Ahlberg, 1989b) suggests that this type of scale ornament is primitive for the Holoptychiidae. *Glyptolepis leptopterus* can be shown to belong in a natural group of small to medium-sized holoptychiids which share certain derived characters, and in this paper the name *Glyptolepis* will be restricted to that clade. The other long-established holoptychiid genera, *Holoptychius* and *Laccognathus*, are both natural taxa based on unambiguous autapomorphies.

The most thoroughly studied porolepiform faunas of the Middle Devonian are those from the Orcadian Basin of Scotland. The fossil-bearing deposits in this region consist of a thick lacustrine sequence, Eifelian to Givetian in age (Donovan, Foster and Westoll, 1974) and capped by fluviatile sediments. Geographically, the deposits fall into two distinct groups, the flagstones of Caithness and Orkney and the nodular beds of the Moray Firth area. The flagstones represent the central parts of the lake basin; they are thicker in Caithness than in Orkney (Trewin, 1986), which suggests that the deepest part of the basin lay in Caithess. The nodular beds are much thinner than the flagstones and lie immediately on top of fluvial deposits. They are marginal, and were presumably deposited during periods of maximum transgression.

The earliest porolepiforms known from the Orcadian basin occur at the so-called 'Achanarras horizon', a transgressive stage represented in central Caithness by the Achanarras fish bed, in Orkney by the Sandwick bed (Trewin, 1976) and in the Moray Firth area by the nodular localities of Cromarty, Lethen Bar, Tynet Burn and Gamrie (Text-fig. 5). This horizon is dated to the Eifelian/Givetian boundary (Donovan, Foster and Westoll, 1974). The fish fauna of the 'Achanarras horizon' is relatively diverse: it comprises four genera of placoderms (*Pterichtyodes*, *Coccosteus*, *Homostius* and *Rhamphodopsis*), several acanthodians of different sizes, two osteolepiforms (*Osteolepis* and *Gyroptychius*), the lungfish *Dipterus* and the actinopterygian *Cheirolepis*, and finally two 'problematic' genera, *Palaeospondylus* and *Achanarella*. The fauna shows some degree of regional variation; for example, *Gyroptychius* is absent at Achanarras whereas *Palaeospondylus* occurs almost exclusively at this locality.

Two holoptychiids are known from the 'Achanarras horizon'. *Glyptolepis leptopterus* is a small form (maximum length approximately 40 cm), characterized by a low number of scale rows between the cleithrum and first dorsal fin, whereas *Glyptolepis polysquama* (="*G. paucidens*" in part, Ahlberg, 1989b) reaches



Text-fig. 5: Map of Orcadian Basin rocks. A - Sandwick; B - Thurso; C - Achanarras; D - Cromarty; E - Lethen Bar; F - Tynet Burn; G - Gamrie (from Trewin 1986).

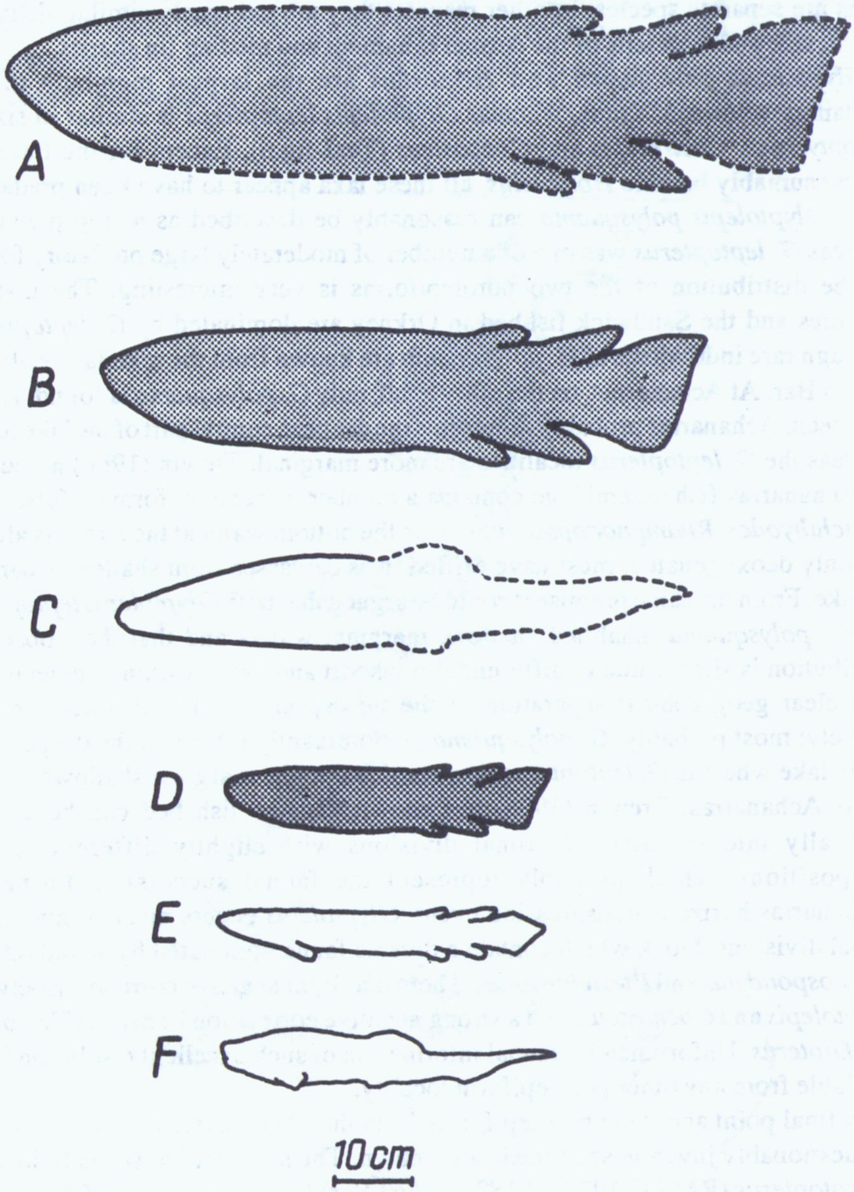
80-85 cm total length and has a higher number of scale rows. The difference in number of scale rows is consistent and shows beyond reasonable doubt that the two forms are separate species. In other respects they are extremely similar, differing only in size and in details of the dermal ornament and median fin shapes.

Glyptolepis polysquama and *Homostius* are the largest members of the 'Achanarras horizon' fauna, whereas *Glyptolepis leptopterus* is similar in size to *Gyroptychius*, *Cheirolepis* and *Coccosteus* (Text-fig.6). Except for the flattened and presumably benthic *Homostius*, all these taxa appear to have been predators. Thus, *Glyptolepis polysquama* can reasonably be described as a 'top predator', whereas *G. leptopterus* was one of a number of moderately large predatory forms.

The distribution of the two porolepiforms is very interesting. The nodular localities and the Sandwick fishbed in Orkney are dominated by *G. leptopterus*, although rare individuals of *G. polysquama* are known from the nodular locality of Lethen Bar. At Achanarras, on the other hand, only *G. polysquama* is found. As we have seen, Achanarras probably represents the deepest, central part of the lake basin, whereas the *G. leptopterus* localities are more marginal. Trewin (1986) noted that the Achanarras fish assemblage contains a number of benthic forms (*Homostius*, *Pterichthyodes*, *Rhamphodopsis*) which, as the bottom water at the site was almost certainly deoxygenated, must have drifted in as carcasses from shallower parts of the lake. From the same premise it could be argued that both *Glyptolepis leptopterus* and *G. polysquama* inhabited shallow, marginal waters and that their observed distribution is simply due to differential transport and preservation. However, the very clear geographical separation of the two species makes this seem highly unlikely; most probably, *G. polysquama* predominantly inhabited the deeper parts of the lake whereas *G. leptopterus* was restricted to the marginal shallows.

At Achanarras, Trewin (1986) has shown that the fish bed can be divided vertically into six distinct faunal divisions with slightly different species compositions, which probably represent the faunal succession during the 'Achanarras horizon' transgression event. *Glyptolepis* occurs most commonly in faunal divisions 2 to 4, which contain a diverse fauna dominated by acanthodians, *Palaeospondylus* and *Pterichthyodes*. There is a slight negative correlation between *Glyptolepis* and *Coccosteus*, and a strong negative correlation between *Glyptolepis* and *Dipterus*. Unfortunately, faunal information of such excellent resolution is not available from any other porolepiform locality.

A final point about the porolepiforms from the 'Achanarras horizon' is that no unquestionably juvenile specimens are known. The smallest known individual of *G. leptopterus* (RMS G 1973.12.182, Lethen Bar) has a total length of 13 cm, and it is possible that smaller carcasses have simply not been preserved. However, the smallest complete specimen of *G. polysquama* (UMZC FCC488, Achanarras) is 38.5 cm long, which cannot reflect preservational bias, as much smaller fishes are plentiful at Achanarras. It is thus clear that the source population(s) of the Achanarras fossils contained only adult individuals of *Glyptolepis*.



Text-fig. 6: The largest fishes from the Orcadian Basin. The porolepiforms are shaded. A - *Asperocephalus*; B - *Glyptolepis polysquama*; C - *Homostius* (conjectural reconstruction); D - *Glyptolepis leptopterus*; E - *Gyroptychius*; F - *Coccosteus*. Note that *Asperocephalus* and *G. leptopterus* were not contemporaries.

The upper part of the Caithness flagstone sequence is well developed near Thurso. Much of the material from this part of the sequence was collected during the first half of the nineteenth century, at a time when the exact provenance of the specimens was often not recorded. As a result, the stratigraphic and geographical resolution of the distribution of different taxa is unfortunately less good than for the 'Achanarras horizon'. The specimens are furthermore often fragmentary.

The general fauna of the upper part of the flagstone sequence is very similar to that of the 'Achanarras horizon', and will not be considered further. As regards the porolepiforms, fragmentary material of *Glyptolepis polysquama* is frequent in the Thurso area (RMS G 1859.33.1365 and 1859.33.1367 are two examples) and is also known from Orkney. *Glyptolepis leptopterus* is not known to occur above the 'Achanarras horizon', but this may simply reflect an absence of fossil- bearing marginal sediments. More important is the appearance of a new porolepiform in these later beds. This form has only recently been recognized as differing from *Glyptolepis polysquama* (Jarvik,1972); material from the two species was previously united under the name "*Glyptolepis paucidens*" (Thomson, 1966). In fact it shares no derived characters with *Glyptolepis*, and is accordingly placed in its own genus as *Asperocephalus milleri* (Ahlberg, 1989b). *Asperocephalus* is a very large porolepiform. One complete skull is known, RMS G 1964.18, which appears to have come from an animal approximately 1 m in length, but the lower jaw RMS G 1896.67.6 derives from a considerably larger individual. This makes *Asperocephalus* the largest fish known from the Orcadian basin (Text-fig.6). The skull is of the generalized holoptychiid type, morphologically very similar to those of *Glyptolepis* and *Holoptychius*, but the postcranial morphology is entirely unknown. *Asperocephalus* is very rare; only six more or less fragmentary specimens are known, all deriving from adult fishes.

To summarize, three holoptychiid porolepiforms are known from the lacustrine sediments of the Orcadian basin, at least two of which co-existed in the lake (or lake system) at any one time. As far as is known, they are all morphologically very similar, but they differ greatly in size. The largest porolepiform at any time was also the largest predator in the fauna, and the smallest was no smaller than any non-porolepiform predator. Where two porolepiforms occur at one locality, the larger species is very rare. The absence of juveniles in the fossil material suggests that the breeding areas may not have lain within the lake basin.

Few other Middle Devonian faunas are known in sufficient detail to show whether more than one porolepiform species is present. However, the *Glyptolepis groenlandica* material from Canning Land, East Greenland (Jarvik, 1972) contains both *Glyptolepis groenlandica* itself (similar in size to *G. leptopterus*) and a much larger, un-named holoptychiid similar to (or possibly identical with) *Asperocephalus*. *Glyptolepis groenlandica* makes up the bulk of the assemblage, whereas the large holoptychiid is only known from a single fragmentary specimen, MGUH VP P 1527A): this pattern is closely reminiscent of that seen in the Orcadian basin. In the Baltic region, a large *Asperocephalus*-like holoptychiid occurs at

Aruküla ("*Glyptolepis*"' Gross, 1941), whereas the recently described *Paraglyptolepis* (Vorobyeva, 1987) is similar in size to *Glyptolepis polysquama.*

Two new porolepiform genera, *Holoptychius* and *Laccognathus*, appear early in the Frasnian. *Holoptychius* first occurs at Scaumenac Bay, where it is associated with *Glyptolepis quebecensis* (=*Quebecius quebecensis*; Schultze and Arsenault, 1987, Ahlberg, 1989b). It is as yet impossible to determine whether there is any size separation between the two taxa, but *G. quebecensis* is approximately the same size as G. *polysquama.* In the fluviatile Lower Frasnian of the Baltic States, *Glyptolepis baltica* occurs together with *Laccognathus panderi* (Gross, 1950). This is a situation quite similar to that in the Givetian of East Greenland and Scotland, for in terms of size *Laccognathus* corresponds closely to *Asperocephalus*, whereas *Glyptolepis baltica* is similar to *G. polysquama.* As can be seen, the small and medium-sized holoptychiids in Givetian and Frasnian faunas nearly all belong to the genus *Glyptolepis.* The large forms *Asperocephalus* and *Laccognathus* are apparently not closely related; it is possible that large size is a primitive holoptychiid character.

One feature which sets the Frasnian assemblages apart from earlier faunas is the presence of large osteolepiforms. At Scaumenac Bay the eusthenopterid *Eusthenopteron* is similar in size to the porolepiforms, whereas the panderichthyid *Elpistostege* seems to be considerably bigger (Schultze and Arsenault, 1985). In the Baltic assemblages, the panderichthyid *Panderichthys* is marginally bigger than *Laccognathus. Panderichthys, Laccognathus* and *Asterolepis* occur together in the mass-death deposits at Lode in Latvia (Lyarskaya and Mark-Kurik, 1973), an interesting association in view of the positive correlation between *Glyptolepis* and *Pterichthyodes* at Achanarras (Trewin, 1986).

The later part of the Late Devonian shows a decline in porolepiform diversity; during the Famennian the group appears to be represented only by the ubiquitous and abundant genus *Holoptychius*, although *Laccognathus* (together with *Panderichthys*) is anomalously recorded from the uppermost Famennian deposits of the USSR (Lyarskaya, 1981). *Holoptychius* varies greatly in size. The material from Dura Den (Famennian, Scotland) is dominated by individuals as small as *Glyptolepis leptopterus*, whereas the *Holoptychius* of Scat Craig (Upper Frasnian, Scotland) must have grown at least as large as *Asperocephalus*, to judge by the huge scales found at this locality (personal observation). By analogy with *Glyptolepis*, it seems highly probable that the genus *Holoptychius* contained several morphologically similar, size-segregated species, although there is as yet no positive evidence of this. In many of the Famennian faunas, *Holoptychius* is associated with very large eusthenopterids (*Eusthenodon* in East Greenland; *Eusthenodon*, *Hyneria* and the rhizodont *Sauripterus* in Eastern North America; Thomson, 1976b), and thus did not occupy a 'top predator' position. As far as is known, the porolepiforms became extinct at the Devonian/Carboniferous boundary, at approximately the same time as the arthrodires, antiarchs and eusthenopterid osteolepiforms.

Discussion

The available evidence creates a picture of the porolepiforms as a group of moderately large to very large piscivores, specialized for rapid acceleration and manoeuvring, and probably using their highly developed sensory line systems for prey detection. At one time or another during the Devonian, porolepiforms occurred together with agnathans, arthrodires, antiarchs, acanthodians, lungfishes and 'rhipidistians'; the only consistently negative correlation seems to be with actinopterygians (except *Cheirolepis*). Porolepids are known both from marine and freshwater deposits, whereas holoptychiids appear to have been restricted to freshwater and possibly estuarine or lagoonal environments. During the Middle Devonian, holoptychiids seem to have held the 'top predator' positions in most of the faunas where they occur, but by the Late Famennian they were co-existing with considerably larger eusthenopterid osteolepiforms.

The two most striking features of porolepiform evolutionary history are morphological conservatism and low taxonomic diversity. The only major morphological shift to occur within the group seems to have been that from the porolepid to the holoptychiid skull pattern, which involved apparently synchronous changes in skull roof and cheekplate proportions, lower jaw morphology and parasymphysial dentition. Neither the porolepids nor the holoptychiids show any sign of morphological 'trends': the porolepid lower jaws from the Siegenian of the Rhineland (Gross, 1936, 1941) are closely similar to those from the Emsian of the Holy Cross Mountains (Kulczycki, 1960), and the skull and body proportions of the Lower Givetian holoptychiid *Glyptolepis polysquama* are virtually indistinguishable from those of Upper Famennian specimens of *Holoptychius*. Within the holoptychiids, which are better known than the porolepids in this respect, most of the observed evolutionary changes concern minor features like dermal ornament and could well be non- adaptive modifications caused by genetic drift. The conservatism of the porolepiforms can be illustrated by comparing them with the osteolepiforms.

The two groups are similar in overall morphology, and where they occur together in the same fauna they tend to show comparable levels of diversity ('Achanarras horizon' - two holoptychiids and two osteolepids; Scaumenac Bay - two holoptychiids, one eusthenopterid and one panderichthyid; *Remigolepis* Series of East Greenland - one holoptychiid, one eusthenopterid). However, the osteolepiforms show much greater variation in skull and body proportions, and the total number of osteolepiform genera seems to be much greater. The most plausible explanation for these differences is that the porolepiforms were subject to stronger evolutionary constraints than the osteolepiforms. The nature of these constraints is less certain, however; genetical and behavioural factors are both possible, but leave no fossil record. The low taxonomic diversity of porolepiforms probably relates directly to the morphological uniformity, as it would be difficult for a number of morphologically very similar porolepiform taxa to co-exist in the same environment without excessive niche overlap. When two porolepiforms do occur at the same locality, they usually differ greatly in size.

The rapid and complete replacement of the porolepids by the holoptychiids was probably the most important event in porolepiform evolution. In the Baltic succession this changeover follows closely upon the first appearance of typically Middle Devonian faunal elements such as osteolepids and non-marine lungfishes. Similarly, the extinction of the porolepiforms at the Devonian/Carboniferous boundary coincided with a major phase of faunal replacement; a number of the most characteristic Devonian fish groups disappeared at this time, with the result that Lower Carboniferous freshwater faunas have a radically different composition from Upper Devonian assemblages. It thus appears that the major events in porolepiform history were not isolated occurrences, but were linked with changes in the associated fish faunas.

It would be most interesting to determine the reason for the morphological conservatism of the porolepiforms, but it is difficult to see how this could be done. A more promising area for future research would be a detailed investigation of the variation in taxonomic and morphological diversity during the history of the group. At present it appears as though the porolepiforms reached a peak of diversity during the Givetian and early Frasnian, but this is almost certainly an artifact caused by the existence of well-preserved and intensely studied faunas from this period. A detailed study of pre-Givetian and Famennian taxa should remove the bias which exists at present, and might also lead to a greater understanding of the ecological interactions between the Porolepiformes and the other groups of Devonian fishes.

Addendum

Since the presentation of this paper, Dr. J. A. Long (Western Australian Museum, Perth) has pointed out to me that porolepiforms have been found at several Australian localities. The material includes well-preserved scales from the Emsian of Taemas, noted by Young (1985). This strengthens the case for a world-wide distribution of the Porolepiformes.

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Gnathorhiza (Dipnoi): life aspects, and lungfish burrows

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Abstract. The dipnoan *Gnathorhiza* is an exceptional fossil. The quantity of skeletal remains is small, but the presence of burrows attributed to *Gnathorhiza* allows the study of many aspects of its lifestyle, not normally known for other fossils. A literature review summarizes the living aspects of *Gnathorhiza* into interpretations based on body fossils (toothplate, sensory, and respiratory information) and trace fossils (ecology, morphology, behavior, and physiology).

The rejection of lungfish origin for structures interpreted as lungfish burrows from the Triassic and Devonian of North America and Great Britain is suggested. This is based on the absence of lungfish remains in any of the structures.

Basic criteria for the separation of organic burrows from inorganically produced structures include consideration of the degree of variation and constraints imposed on organically produced artifacts.

Introduction

Gnathorhiza is a small to medium-sized fish (estimate: 5-50 cm) known from teeth collected from late Paleozoic deposits in the USA and early Mesozoic deposits of the USSR. Numerous trace fossils (burrows) in the mid-continent of the USA and early Mesozoic deposits of the USSR. Numerous trace fossils (burrows) in the mid-continent of the USA (Kansas, Oklahoma, Texas, New Mexico) contain remains of this genus and provide data for the interpretation of behavior, physiology, and ecology.

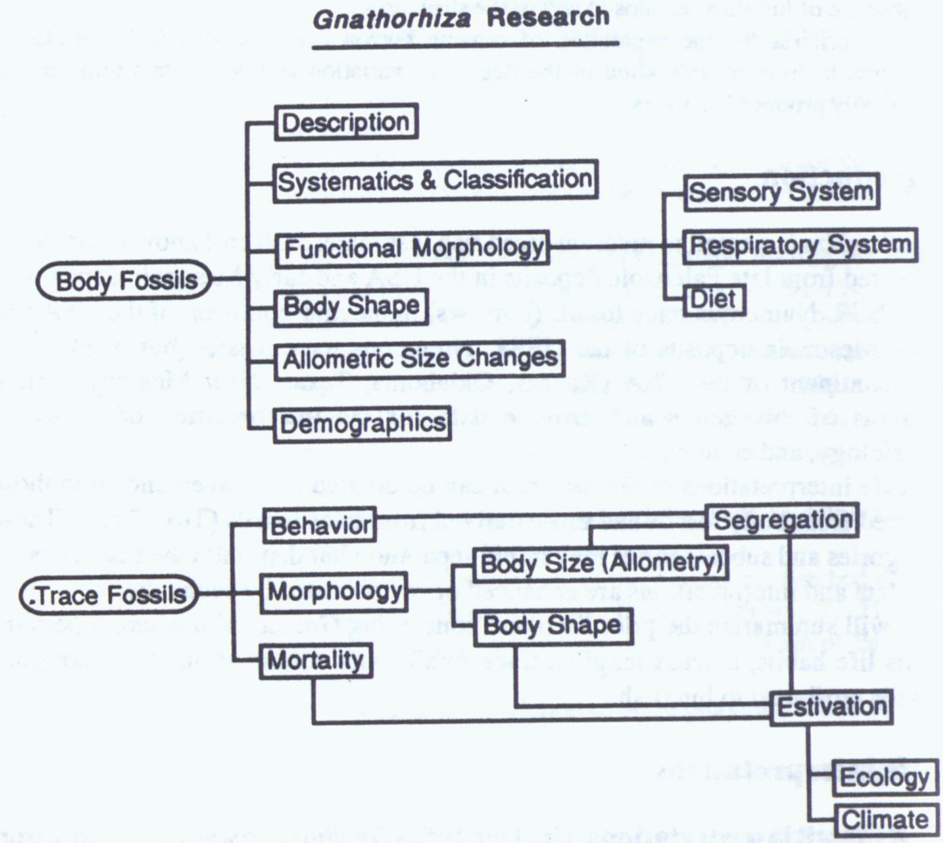
Life interpretations of *Gnathorhiza* can be divided for convenience into those derived from body fossils and those derived from trace fossils (Text-fig. 1). These categories and subcategories may imply separation but that is not the case. Most of the data and interpretations are enhanced or corroborated by each other.

I will summarize the prior literature concerning *Gnathorhiza* where it pertains to its life habits, discuss lungfish trace fossils, and comment on Devonian trace fossils attributed to lungfish.

Life interpretations

Body fossil interpretations. Until the 1950s *Gnathorhiza* was known only from toothplates. Skull material has since been recognized, increasing the knowledge of life habits, but toothplates are still numerically greater. The most unusual discussions of *Gnathorhiza* biology relate to the functional morphology deduced from non-toothplate cranial material. Discussions include: sensory input and respiratory ability.

Toothplates. The shearing teeth of *Gnathorhiza* are so unusual for fossil dipnoans that specific attention was drawn to them by Eastman (1903) in the title of his paper "A Peculiar Modification Amongst Permian Dipnoans". He compared the shearing teeth to those of sharks. Berman (1968) compared the teeth and jaws to other lungfish. He considered them to be more similar to *Neoceratodus* and *Ceratodus* than to the lepidosirenids. He concluded that plant material was a very important component of the gnathorizid diet. Food webs created by Olson (see Olson, 1977, for an example) describe a hypothesized flow of food through the trophic pyramid, including *Gnathorhiza*. Olson considered aquatic invertebrates to be a principal source of food with plants and small vertebrates supplementing the diet.



Text-fig. 1. Relationship of data and research categories for life interpretations of *Gnathorhiza*.

Large samples of toothplates document the size changes and presumably allometric growth. Carlson (1968) noted that small teeth have distinct and numerous denticulations as compared to larger teeth. Sharp edged tooth units are added onto the distal ends of the toothplates, creating a serrated pattern on the cutting edge. The decline in denticulation number with increasing size is related to wear. Carlson (1968) also noted changes in the ridge length with size.

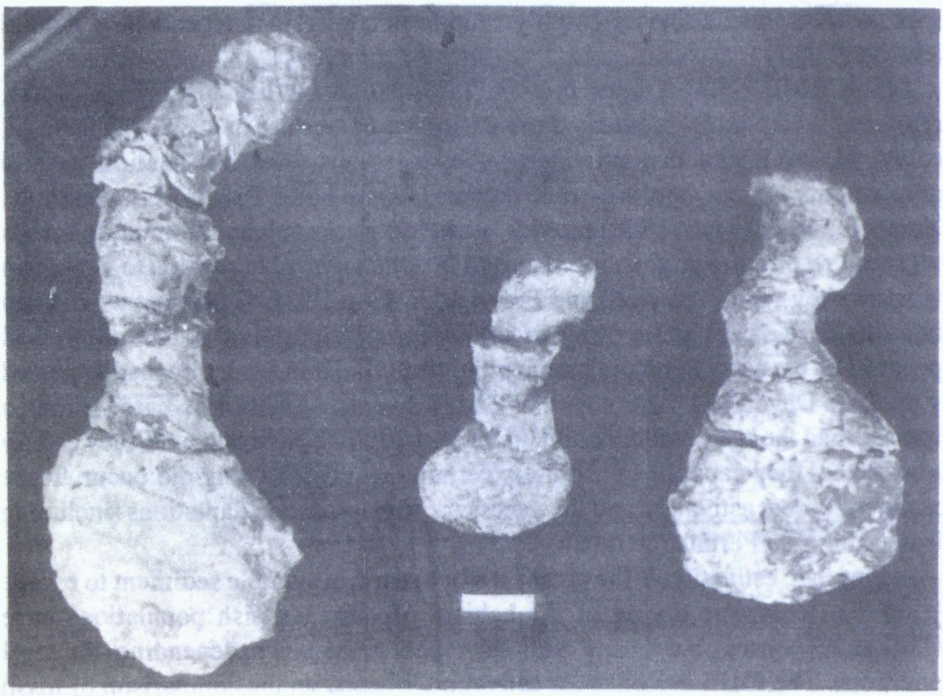
Sensory system. Berman (1976) discussed the relative sensitivity of the lateral line system of *G. bothrotreta*. The lateral line of gnathorhizids is embedded in an open groove on the skull- roof bones, not buried in the bone like in early dipnoans or in the skin above the bone like in modern dipnoans. *G. bothrotreta* has open grooved lateral lines, except in the K-M bone. The K-M bone is situated in the postero-lateral part of the skull, behind the orbit. Here the lateral line is buried in the bone with opeOnings that communicate to the surface. The bilateral position on the skull roof and the separate openings are hypothesized to create extra sensitivity to directional hearing. Incoming vibrations strike the separate nerve endings at different and discrete times.

Respiratory system. Comparison of modern lungfish respiratory adaptions with *Gnathorhiza* reveals many functional similarities (Campbell and Barwick, 1988). Included are: elongate and expandable buccal cavity (based on the long, wide parasphenoid, flexible skull, and reduced cheek region); sealibility of the buccal cavity by the tongue (anteriorly located toothplates in buccal cavity); and the ability to expand the buccal cavity (highly mobile ceratohyal, independently mobile cleithrum).

Trace fossil data. Traces provide information on life histories of fossil organisms which are sometimes more definitive and wider in scope (behavioral, ecological, etc.) than that provided by body fossils. The information usually complements or corroborates that deduced from body fossils. For example, Campbell and Barwick (1988) provide morphological evidence from body fossils that aerial respiration might have occurred in *Gnathorhiza*. In regards to Devonian dipnoans they state (Campbell and Barwick, 1988, p. 223): "The most we can say about the time of evolution of air breathing in the Dipnoi is that it certainly had appeared by the early Permian, but facultative air breathing probably had appeared by the Late Devonian." Although they had earlier stated that some Late Devonian dipnoans had the bony evidence and lived in appropriate environments, they clearly indicate that they cannot be absolutely certain that air-breathing did occur. Trace fossils document estivation and the necessary physiological adaptations (including air-breathing) in Permian lungfish.

In lungfish, estivation is the creation of a burrow in suitable sediment to escape a partial or complete drying of the habitat. Modern lungfish populations have different responses and create various types of burrows depending on local conditions. The fossil evidence for estivation is based on the comparison of fossil to modern burrows. Unfortunately, the modern analogs are not very well known. The flask-shaped burrows from the Kansas Permian (Text-fig. 2) are almost certainly estivation burrows based on their similarity to modern lungfish burrows. The cylindrical burrows from the Permian of Texas, New Mexico and Oklahoma are also likely to be estivation burrows. The morphology is less diagnostic but the evidence for size segregation (Carlson, 1968), mortality, and high densities is consistent with modern estivators (McAllister, manuscript). The cylindrical burrows may not have been as effective for as long or for as intensely dry conditions as the flask-shaped burrows, or the body shape of these lungfish was too stocky to coil in a flask.

Ecological considerations. Lungfish burrows have been used to refine climatological and environmental aspects of the past. Alternating wet-dry seasonality in suitable habitat is stated or implied by every estivation burrow publication since the first description by Romer and Olson (1954). Romer and Olson (1954), and Romer (1958) suggested that increasing aridity occurred in the Texas Permian. This correlated with the replacement of *Sagenodus* (a non-estivating lungfish) by *Gnathorhiza* with burrows in the younger more seasonally arid units. Vaughn (1964) suggested an earlier onset of arid conditions in the Permian bed of New Mexico (compared to the Texas beds to the east) based on the burrows found there. Berman (1970) worked in the Texas Permian where both *Sagenodus* and *Gnathorhiza* occurred. He suggested that this was an area with a transitional climate. *Gnathorhiza* occurred in the stream deposits while *Sagenodus* was in the



Text-fig. 2. Flask - shaped lungfish burrows from the Permian age Speiser Shale of Kansas. Scale bar equal to 1 cm.

lake deposits. This proably reflected ephemeral conditions in the streams while the lakes did not dry completely. Berman (1976) also discussed seasonality in New Mexico in regards to burrows he found there.

Most of the important ecological inferences concerning the Permian of Texas were originally discussed by Olson. For example, Olson (1952) discussed the evolutionary framework of the fauna, including *Gnathorhiza*, through Permian time. More specific discussions of *Gnathorhiza* are present in a summarization and comparison of different Oklahoma Permian lake deposits by Olson (1977). In the deposits interpreted as semipermanent (subject to seasonal drought), *Gnathorhiza* was abundant. The high frequency, low faunal diversity, cohabitors (*Lysorophus* and *Diplocaulus*), and food web relationships were all considered.

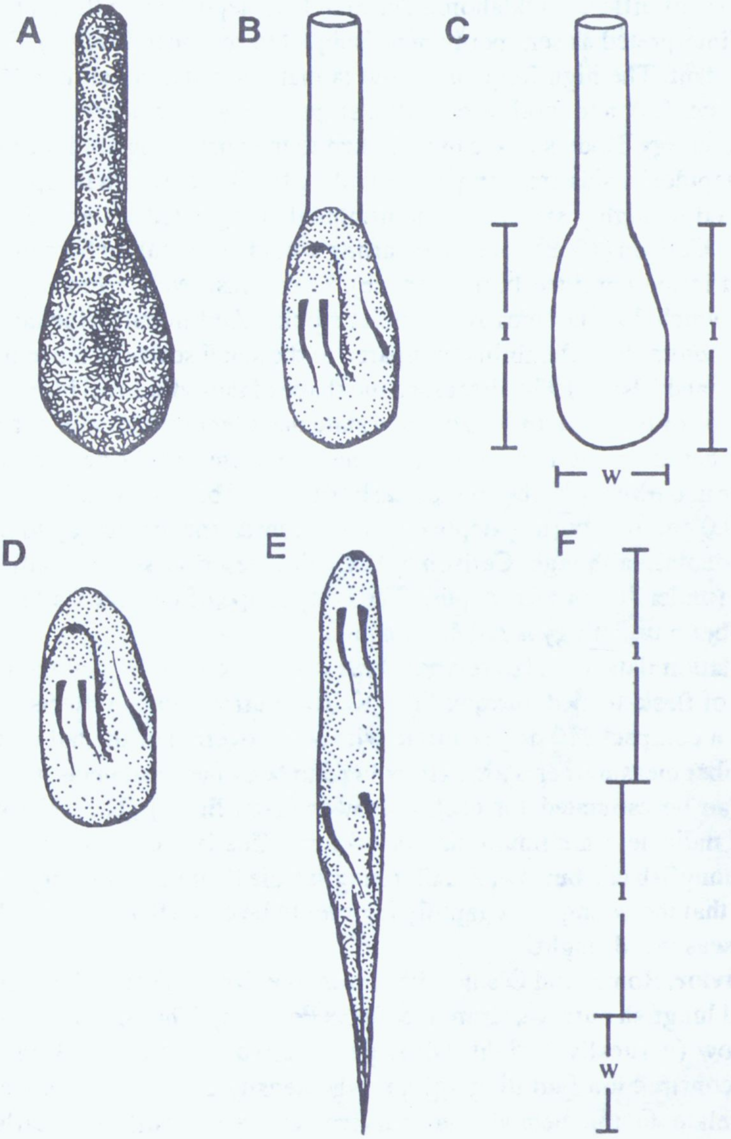
Morphology. Body shape can be linked to the burrowing ability of the animal. Modern lepidosirenids are elongate, providing flexibility which is especially useful in confined or highly structured environments (vegetated waters of swamps for example). Carlson (1968) noted that curling would be useful for burrowers (to twist and bend in the confined burrow space). In contrast, *Neoceratodus*, the modern lungfish which does not burrow, is rather stocky. Additionally, the large scales of *Neoceratodus* reduce flexibility compared to the small scales of the lepidosirenids.

Romer and Olson (1954) discussed the shape of the cylindrical burrows in regard to the shape of their *Gnathorhiza*. They state that *Gnathorhiza* was not slender and fusiform based on the burrow shape. The fish seem to be oriented head-up and tail-down in the burrow. The cylindrical burrows and bony contents tend to be larger (up to 69.0 cm total burrow depth) than the Kansas specimens (up to 6.0 cm total burrow depth), although Carlson (1968) did describe some small cylindrical burrows (under 10 cm total depth). The body shape of the Kansas lungfish based on chamber morphology is rather elongate.

Population data and size relationships can potentially be gathered from large samples of flask-shaped burrows. The Kansas burrow shape reflects the ability to curl into a compact 360 degree circle with some overlap of the tail on the head. If the chamber measurements are extrapolated to body measurements, then total body length can be estimated for each burrower (Text-fig. 3). The observed Kansas burrows indicate a minimum size of 50 mm. This is the smallest size at which modern lungfish can burrow. Smaller lungfish die if stranded in a drying puddle. It is likely that the young grow rapidly in order to be of sufficient size to burrow and survive seasonal drought.

Behavior. Romer and Olson (1954) were the first to discuss the implications of the fossil lungfish burrows (from the Texas Permian). The posture of the animal in the burrow (vertically upright, tail slightly curled at the bottom), the method of burrow construction (tail digging), and the density of the burrows are all factors which relate to the behavior to survive adverse conditions. Carlson (1968) considered some other behavioral aspects such as segregation by size, and burrowing by chewing. The Kansas burrows are easier to compare directly to modern analogs and allow more specific and confident analysis.

Physiology. The ability of modern lungfish to estivate requires a physiological shift from activity to torpor. Metabolism slows and shifts, respiration is totally aerial and slow, etc. Estivation burrows from the past imply similar adaptations. Sometimes the estivators were not strong enough to survive. Mortality data was gathered by Romer and Olson (1954), Carlson (1968) and McAllister (manuscript).



Text-fig. 3. Estimation of lungfish dimensions from burrow casts. A) The burrow cast. B) Reconstruction of lungfish within burrow. C) Measurement of burrow chamber. D) Curled lungfish reconstruction. E) Uncurled lungfish reconstruction. F) Estimate of total length.

Lungfish burrows

Triassic.

In addition to those from the Permian, lungfish burrows are described from many other ages and localities (Text-fig.4). Structures interpreted as lungfish burrows occur in the Triassic age Chinle and Dolores Formations in Utah, Arizona, Colorado, and New Mexico (Dubiel et al., 1987). I wrote a discussion article (McAllister, 1988) reviewing the characteristics of fossil lungfish burrows which contain lungfish and contested the identification of the Triassic structures.

Text-fig. 4. Location of fossil lungfish burrow reports. D= Devonian; Pn= Pennsylvanian; P= Permian; T= Triassic; C= Cretaceous (see Fuchs-Parker, 1977); O= Oligocene (in Dubiel et al., 1987).

McAllister (1988) recommended that burrows attributed to lungfish be limited only to those with lungfish inside, and similar associated burrows. For example, there may be ten burrows at a locality. If one borrow contains a lungfish and the other nine are similar to that burrow, then I assume that they all are lungfish burrows. Likewise, similar burrows in the same horizon are also likely to be formed by lungfish. Such determinations may be subject to error; Olson and Bolles (1975) described similar burrows from one locality, one lungfish and one unknown - possibly crustacean. In such cases the attribution depends on the acuity and judgment of the describer.

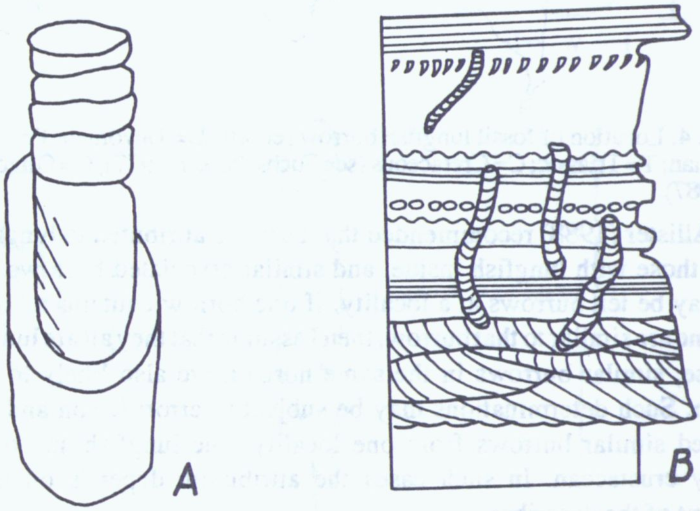
McAllister (1988) also summarized characteristics of known fossil lungfish burrows that could be used for comparisons to unknown structures (Table; Text-fig. 5A). If these characteristics and other lines of evidence were indicative, then a lungfish origin can be tentatively assumed without lungfish being present. However, this judgment will always be somewhat suspect. Other forms and characteristics of fossil lungfish burrows will no doubt be described in the future, and comparisons can also be made with modern lungfish burrows. Unfortunately, modern burrows are not characterized in as much detail as the fossil burrows, and are thus difficult to assess and apply as a modern analog to the fossil condition.

Table

General characteristics of cylindrical lungfish burrows
Shape: cylindrical, circular cross-section, hemispherical bottom
Vertical orientation
Distinct sides and bottom
Spiral striations
Periferal sediment compaction
Weathering into stacked disks

Infill: harder, more calcareous, larger grained
Matrix: softer, less calcareous, smaller grained

Associated sedimentary structures - consistent with seasonality
Associated fauna and flora - xeric, low diversity



Text-fig. 5. Cylindrical burrows. A) Reconstruction with some characteristics of lungfish burrows described from the Texas and Oklahoma Permian. Note the weathering, resistant infill, striations, and compaction zone (at the base). B) Geologic section of Devonian structures. Note the menisci, and the variety of sedimentary depositions. Modified from Allen and Williams (1981).

Dubiel et al. (1988) reaffirmed their original conclusions that the Triassic structures were best interpreted as lungfish burrows and in summary state: "...McAllister presents no compelling evidence that the Triassic ichnofossils are not lungfish burrows; he merely reiterates our observation that they contain no fish remains." Dubiel et al. (1988) did address specific points which I brought up in the discussion (McAllister 1988). Two of these points deserve special attention. For the first point, the necessity for lungfish remains to be present was questioned in the identification of lungfish burrows. Many reasons were provided to explain the problem of no lungfish remains in the burrows (most important was cited bone destruction by sediment conditions). However, the question should be: What is necessary and sufficient for a structure to be asserted as lungfish derived? Are enclosed lungfish necessary? What characteristics are sufficient to determine origin if there is no contained lungfish? Even if these are truly lungfish burrows, the combination of no enclosed lungfish and lack of demonstrated lungfish characters make doubtful their assignment to lungfish.

The other point I wish to consider concerns the variety of sediments and inferred habitats in which the structures occur. Dubiel et al. (1988, p.367) state: "Holocene lungfish bones are reported from lime mud, siliciclastic mud, and sand (Greenwood, 1987), and thus are excellent analogues for Chinle and Dolores ichnofossils." The Triassic burrows occur in a variey of sediments including granulitic sand. Living lungfish live in a variety of habitats, covering many depositional evironments. Because of this "...one should wonder why occurrences of Paleozoic lungfish burrows, especially those of the Permian, are reported in such small numbers and occur in such restricted lithologies."

Fine-grained sediments are typical of the matrix surrounding fossil and modern lungfish burrows. The occurrence of lungfish burrows in sand, however, is unusual and is documented within Greenwood (1987) for only thee modern cases.

The first case of a sandy burrow is a shallow scoop nest used for breeding by a specimen of *Protopterus aethiopicus*. It is a circular clearing in the vegetation, which is slightly sunk into the sandy substrate. Another burrow of *P. aethiopicus* is described as follows (Greenwood, 1987, p.171): "There was a submerged chamber approximately 800 mm deep and 250 mm in diameter formed in the coarse sand and gravel lying against a fallen and partly submerged trunk of an ambath tree; the completely subaquatic entrance channel ran below and along the length of the trunk and was connected with a nearby creek." The third nest was formed by a specimen of *P. amphibious*. It is described as follows (Greenwood, 1987, p.169): "Another specimen was found in the moist sand of a dry water-course... No cocoon had been formed, but other details about its condition are unavailable (Trewavas, '54)."

The scoop nest is morphologically dissimilar to the fossils and is described in other modern reports. However, it has not been reported before on sandy substrates. The other two burrows are notable precisely because they are unusual, and unexpected in a sandy substrate. I suspect the tree trunk was an integral supporting structure of the second burrow, and that this lungfish would not have burrowed into a sandy gravel except for some unusual circumstance (use of an abandoned burrow). The third burrow does not have enough associated data for interpretation. This lungfish may have been trapped in a sandy substrate under unusual circumstances, with little hope for survival.

None of these three burrows is comparable to the structures described by Dubiel et al. (1987), or possess enough data for proper comparison. These modern examples of sandy burrows are apparently uncommon and are not useful analogs for the Triassic structures. Finally, although lungfish can occur in many environments, burrows seem to be restricted to environments suitable for specific purposes. The estivation burrows require specific qualities in the mud matrix. It has to be firm enough to provide some resistance, yet soft enough to chew into, and also to be of a consistency that will dry without cracking though the fish.

Recent developments concerning the Triassic structures are of great concern to the question of burrow producers. Steve Hasiotus (University of Buffalo, Buffalo, New York) has collected some of these structures with crustacean remains. He will describe the crustacean and their burrows. Finally, the variability of the Triassic burrows, and the distinct morphologies present, would lead me to consider the likelihood that there may be more than one agent in their production.

Devonian age burrows

Lungfish burrows have also been reported from the Devonian sediments of North America and Great Britain. Reports include: Woodrow and Fletcher (1968), Donovan et al. (1978), O'Sullivan et al. (1986), and Benton (1988). None of the burrows cited have lungfish remains associated with the burrows. Woodrow and Fletcher (1968) provide a short account of the Upper Devonian structures from Pennsylvania, USA in an abstract. Later, Woodrow et al. (1973, p.3057) state that burrows are: "...strikingly similar to those reported from the Texas Permian by Romer and Olsen [sic] 1954."

In these cases, the lack of lungfish remains is the primary concern in my acceptance of Devonian lungfish burrows. Although assignments are usually described as tentative, this is still too liberal an interpretation. Secondarily, the descriptions are vague and generally refer to similarities with the Permian age burrows without providing specifics. Large size, structureless fill, and occurence in a depositional environment consistent with aridity or seasonality all are cited as evidence. Additionally, the biological understanding of the living and fossil dipnoans is often oversimplified, based on incomplete accounts or misconceptions, thus compromising the interpretations futher.

For example, O'Sullivan et al. (1986, p.904) cite the following in their argumentation for Devonian lungfish burrows from Ireland: "It is thought that the three extant genera are morphologically and behaviorally similar to their Devonian ancestors (McFarland et al., 1979). Extant forms frequent areas that flood during the wet season and unlike other fishes, aestivate during periods of drought... Fossil burrows containing lungfish tooth plates have been found in the Devonian, Carboniferous and Permian of North America and Europe (Romer, 1947; Romer and Olson, 1954; Carlson, 1968; Lund, 1970, 1973; Berman, 1976; Scott et al., 1976; McFarland et al., 1979)."

The information quoted is traced to McFarland et al. (1979), a textbook which does not provide specific citations to the primary literature. This reference also states that fossil lungfish are poorly ossified (like modern ones) and so do not preserve well except due to self-burial in burrows. Such statements perpetuate popular misconceptions that all lungfish are the same. Fossil lungfish are typified by robust skull roofs, and only a few of the known fossils are from burrows. Fossil lungfish burrows are not as well known either in time or location as suggested. Fossil burrows with lungfish remains are restricted to the Permian of Kansas, Oklahoma, Texas, and New Mexico. Statements implying otherwise are not based on primary published accounts of which I am aware.

Other problems with these statements include narrow consideration of the modern analog. A popular misconception of lungfish is that all are capable of estivation, that they all live in seasonal environments, and that all fossil lungfish are similar in habit to the modern forms. Not all lungfish are estivating swamp-dwellers. *Neoceratodus* is rather stocky with large scales. It is not known to estivate. The lepidosirenids are eel-shaped with small scales. They are capable of estivation. The Devonian lungfish have the stocky shape similar to *Neoceratodus*, and on that point can not as easily curl and twist into a compact burrow. The range of environments in which the lepidosirenids live include not only swamps, but also perennial lakes and rivers. The behavior of these lungfish can also mitigate against estivation. Some lungfish which live in ephemeral environments leave when the water recedes, or only adult males will estivate.

A problem caused by a poor data base is illustrated by the short summary article by Benton (1988) concerning vertebrate burrowing through time (with the emphasis on behavioral evolution). He relates that the most common fossil burrows, considered to be formed by lungfish, occur as far back as the Devonian. The flask-shaped estivation burrow of *Protopterus* is implicitly described — the body is curved, and the mucus envelope is formed with a small opening at the mouth to allow breathing. Then Benton (1988, p.17) states: "Only a few fossil lungfish burrows contain the bones of lungfish[1-3], but the shape of the burrows and their relationship to the sediment indicate their origin (Fig.1)." Figure 1 refers to burrows from the Early Devonian of South Wales. The figure was modified from Allen and Williams (1981) who described the burrows as *Beaconites antarticus* (Text-fig. 5B). Allen and Williams (1981) discussed possible origins of the burrows from a historical perspective. Lungfish were not discussed although mention was made earlier in the paper to similar structures described by Donovan et al. (1978) as Devonian lungfish burrows from Scotland. Possible producers were considered to include invertebrates and even amphibian or reptiles, but no firm conclusion was possible.

Unfortunately, the shape of the fossil burrows (cylindrical, not flask-shaped as implied) discussed by Benton (1988) is undiagnostic by itself as lungfish. Even the flask-shaped burrow shape by itself could potentially be confused with burrows of other animals. The sedimentary relationships in the figure are also suspect if it accurately portrays a non-mud matrix.

Poor data concerning fossil burrows leads to error in interpretations and synthesis. Not all structures identified in the literature as lungfish burrows are actually created by lungfish. There is a tendency to identify ambiguous cylindrical structures with no easily appended creator to be of lungfish origin, especially when found in a facies interpretable as a dry or seasonal environment. The only lungfish burrows that should be considered at this time for data analysis should be modern forms, and the well described Permian age burrows which include representatives that contain lungfish.

Recognition

It is important to have a clear understanding of what is interpreted as a lungfish burrow. This is important because further interpretations have often broad implications (ecological, physiological, etc.). Informal reports (to me) have indicated confusion of sedimentary features and weathering patterns with lungfish burrows. Initial consideration begins with the likelihood of a biological origin. Biologically produced structures will reflect characteristics and restraints of the producer. Pseudotraces will not be confined by biological constraints. One reported lungfish burrow site was a roadcut with highly calcareous resistant mudstone layers alternating with less calcareous mudstones. The surface of the calcareous mudstone weathered into vertically oriented "burrows". They were densely packed but had no cutting intersections. The calcareous layers merged with other calcareous layers in a few instances, crossing through the less calcareous layers. The structures lacked any particular shape except for being rounded and generally vertically elongate. Some structures were bifid or trifid, some were externally angular. The structures did not recognizably extend into the outcrop and, most significantly, did not appear to have any size relationships or constraints. Some of the more extreme examples include width to lengths as follows: 0.5:30 cm; 5.0:5.0 cm; 6.0:13.0 cm. Attributing the variation to an organism is difficult, whereas weathering of the unit is easily acceptable.

Another example of an informal report is most easily interpretable as weathering of fossil soil peds. Weathering in a fossil soil unit produced cylinrical structures in vertical relief. These were less random in size range but were still more variable in morphology than products of living organisms. Again, the weathered surface was dramatically different from the inner surface. The inner surface was angular and separated along soil cutins which were indistinguishable from the unweathered unit.

The burrows from Kansas reflect the size and shape of their creators. These burrows contained tightly coiled lungfish whose body forms were cast by the chamber. Trends can be seen in measurements of the chambers. These reflect size changes in the organisms which made the sampled burrows. The density of the flask shaped fossil burrows also corresponds to modern estivating burrow densities.

Although variation is expected in burrows, the degree should reflect the burrow-makers' shape, allometric growth, population structure, burrow construction, habit changes or other biological aspects. In essence, weathering patterns and sedimentological features tend to be more random in size and shape, surface details change or disappear deeper in the outcrop, and sharp, smooth and clear boundaries are lacking. Occurrence of structures in a wide variety of environments, or composed of a wide variety of different material should also be viewed cautiously. Organisms and their artifacts generally are suited best to narrow environmental conditions.

Conclusions

Gnathorhiza is represented by both body and trace fossils. This allows a wider array of research using different approaches. Trace fossils can corroborate (respiratory mode — Campbell and Barwick, 1988) or provide new information. Trace fossils document the producers' actions — providing information concerning the living habits. In the case of *Gnathorhiza* this includes estivation, physiology, behavior and ecology.

Not all fossil "lungfish burrows" described in the literature are actually lungfish burrows. Inorganically produced structures will be extremely variable and will differ dramatically from weathered to unweathered surfaces. Any burrow ought to reflect the constraints of the organism that built it.

Recognition criteria based on similarities to other fossil finds can provide some confidence but the only definitive evidence is to find fossil remains of lungfish in the burrow. In comparisons with modern burrows there are important aspects to consider. They essentially involve the range of habits and the restrictions of modern lungfish. Not all lungfish are capable of estivating, many do not live in habitats where they need to estivate, and some will follow receding waters away from the desiccating habitat to avoid estivation. There is also a great variety of burrows that modern lungfish create. Some are for living or breeding purposes only, some estivation burrows have a radically different form from the classic flask-shaped burrow. Finally, the sedimentary requirements of burrows (especially the flask-shaped burrow) are restricted. Improper sediments will result in mal-formed burrows and increased mortality.

It is desirable to designate as lungfish burrows only those structures which can be clearly demonstrated to be formed by lungfish (McAllister, 1988). The only way to be fully confident of an assignment is if a lungfish occurs within that burrow or similar burrows within the stratigraphic unit. Structures with sufficient similarities to known lungfish burrows may be suspected to have been created by lungfish but confidence in identification and interpretation will have to be much lower. Based on this criterion, only modern and Permian age lungfish burrows are known.

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Functional aspects of the armour in the early vertebrates

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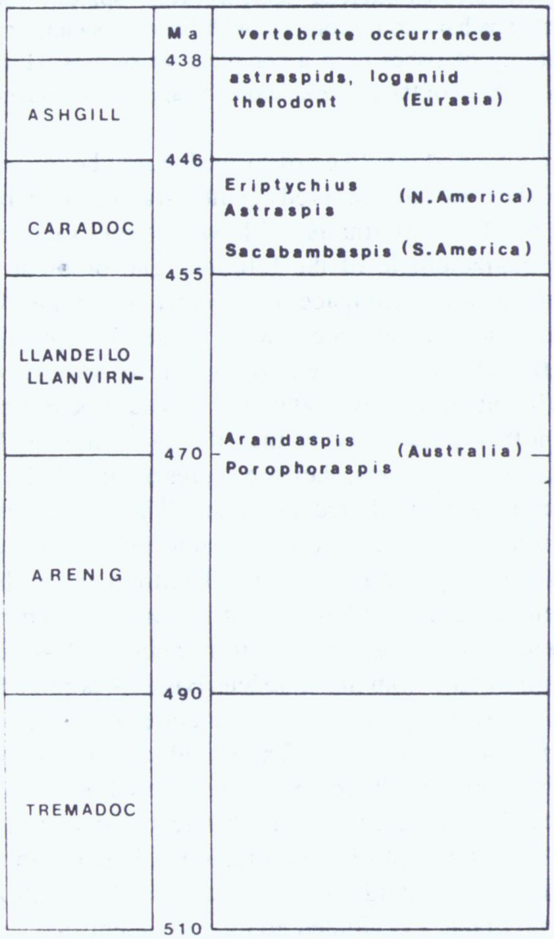
Abstract. The possible factors stimulating the development of carapaces in the early vertebrates are discussed; biological factors are considered as primary. The specific vertebrate assemblages, which most probably formed in the preSilurian times and included higher developed representatives of fishes, e.g. chondrichthyans and osteichthyids, caused the changes in the locomotion of agnathans, and consequently in their body shape. The absence of the paired and some unpaired fins in these vertebrates was to some extent compensated by rigidly fixed exoskeletal elements (keels, spines). Though in rectilinear motion the armoured agnathans could compete with fishes in swimming speed they never reached manoeuvrability of fishes with a complete set of fins. Having exhausted the potential of the development of their exoskeleton, the agnathans became extinct.

The Devonian, often termed the "Age of Fishes" might better be called the "Age of the Armoured Fishes" as the armoured agnathans and placoderms predominated among vertebrates. The agnathans with well-developed carapaces were, nevertheless, also characteristic of the Silurian. The problem is which factors stimulated the development of carapaces in the early vertebrates. One possibility is that their appearance and development were caused by specific environmental conditions, e.g. the chemical content of water. If so, the conditions were fundamentally different from those today and it would be extremely difficult to specify them. Another possibility is that the phenomenon has a biological explanation. As to the placoderms, they are represented only by fossil forms and are not easily comparable with recent fishes. The agnathans comprise both numerous fossil representatives and some recent forms lacking an exoskeleton.

The Ordovician, lasting for more than 70 million years, has revealed few agnathans: the heterostracans and thelodonts. It must be emphasized that the **Ordovician vertebrate finds** are very far from being wide-spread (Text-fig. 1). The two earliest forms come from the Amadeus Basin, Australia, from a unit of late Arenig to early Llanvirn in age and have been collected from two localities (see Ritchie and Gilbert-Tomlinson, 1977). The Caradoc vertebrate localies are more numerous. Still, there are only three genera discovered on two continents, North and South America. The Ashgill of Siberia has revealed some astraspids and the far North-East of Europe (Timan-Pechora region) a loganiid thelodont (Talimaa, 1990). A huge interval, including the Tremadoc and almost all Arenig, i.e. more than half of the Ordovician, has yielded no properly identified vertebrate remains, which naturally does not exclude a lengthy period of vertebrate development in the early Ordovician and before it. In the Silurian several fish groups existed:

chondrichthyans, acanthodians, osteichthyids, and quite probably also placoderms (Text-fig. 2). Obviously these groups had a long preSilurian history (see e.g. Karatajūte-Talimaa, this volume) and formed together with agnathans specific vertebrate assemblages. It is quite probable that the ecological relationships, particularly the predator - prey relationships have largely remained unchanged, whereas the systematic composition of the assemblages has significantly altered during geological time.

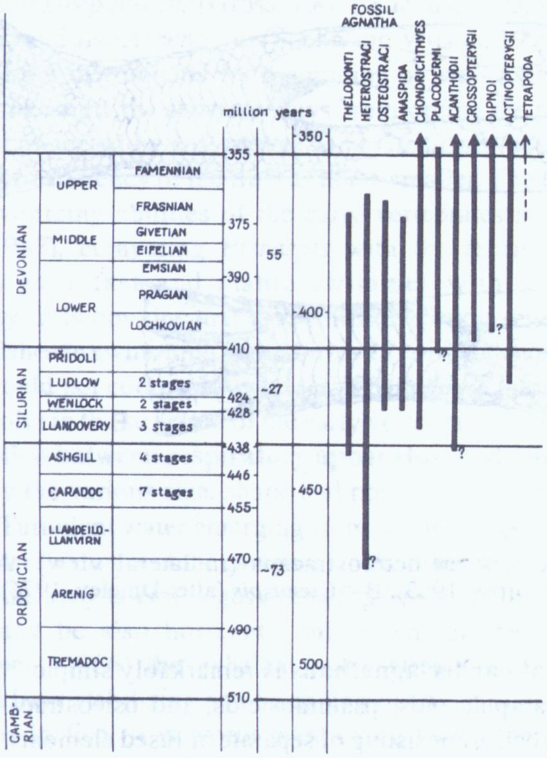
Free-living predatory invertebrates, cephalopods and crustaceans, may have influenced the development of the early vertebrate assemblages consisting mainly of agnathans. But only such organisms could serve as a constant stimulus for the development of agnathans that were on a higher level of evolution, i.e. fishes. Even primitive fishes had enormous and well-known advantages in their structure in comparison with the vast majority of agnathans. They possessed paired appendages



Text-fig. 1. Range of Ordovician vertebrates. Geochronometric data by Cowie and Bassett, 1989.

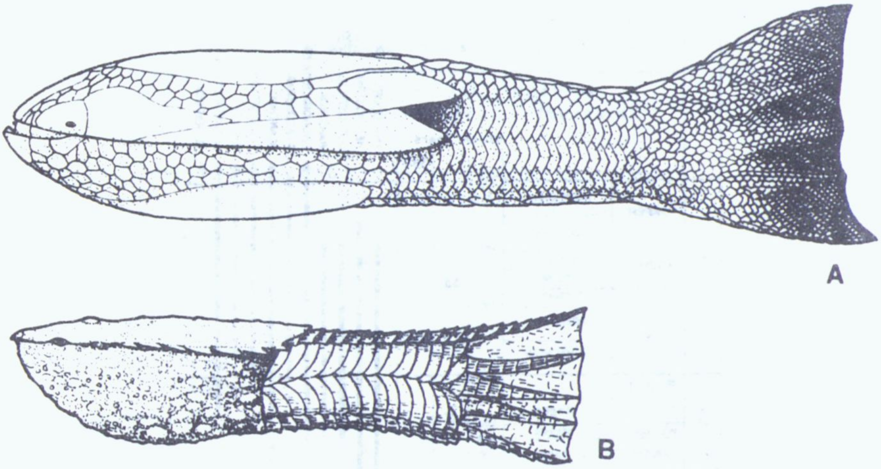
and a vertical column, a jaw apparatus, a better developed brain and sense organs. These qualities enabled them to be more active and to pursue more efficient modes of swimming.

It can be supposed that the earliest agnathans lacking armour had a body-form similar to that of worms (Gutmann, 1984), conodont animals and cyclostomes, and an anguilliform swimming mode, respectively. Living under the same conditions as fishes and belonging to the vertebrate assemblages (and dominating them for a long time) at least several agnathans were to change their type of locomotion and, consequently, to modify their body form. Possessing, however, a low level of



Text-fig. 2. Range of vertebrates in the Silurian and Devonian. Geochronometric data by Cowie and Bassett, 1989.

development, their main potential lay in having skin of a rather complicated structure. It allowed the formation of an exoskeleton to compensate the primitive endoskeleton of these animals. The idea has risen from Yakovlev's statement (1966) that the exoskeleton in fish is a functional analogue of vertebrate column. The result of this compensation is amply demonstrated by a large number of Silurian and Devonian agnathans, particularly heterostracans and osteostracans. The point is that the carapaces of these agnathans should be considered first of all from the aspect of locomotion rather than from the other functions, e.g. protection against predatory fishes, as follows from the traditional and widely accepted viewpoint. Still other functions: protection against ectoparasites, abrasion and other injuries (Reif, 1985), cryptic function of carapace ornamentation and an armour as barrier in water and salt metabolism (Burdak, 1979) are undoubtedly significant.



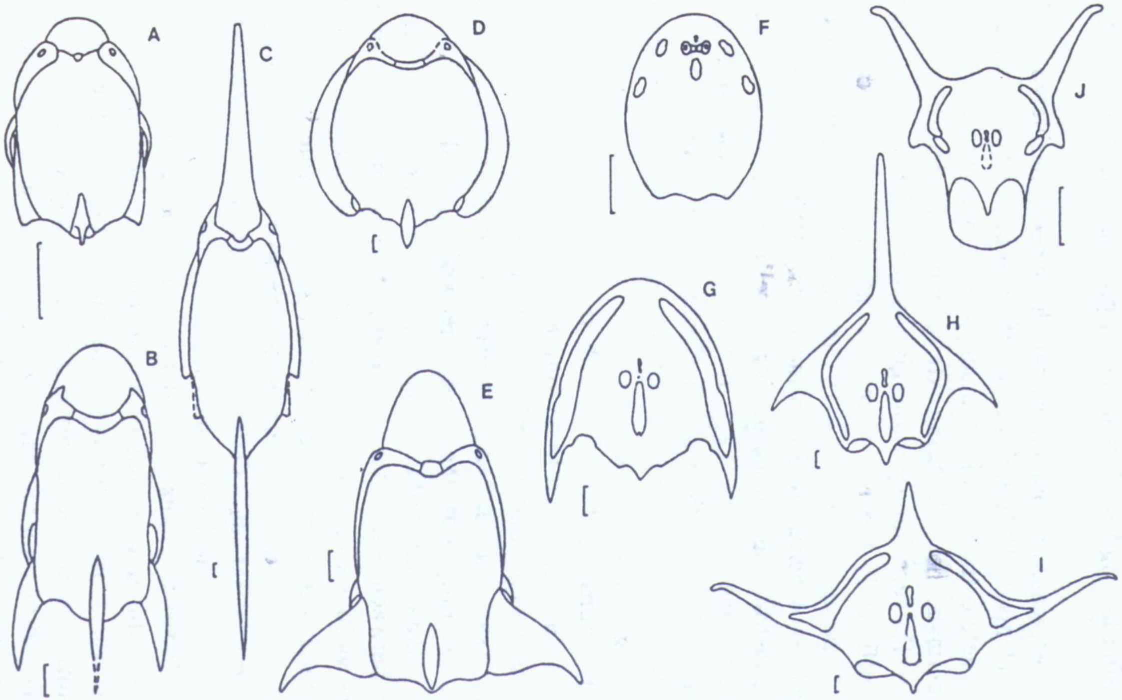
Text-fig. 3. Early Devonian heterostracans (in lateral view): A - *Drepanaspis gemuendenensis* (after Gross, 1963), B - *Ctenaspis* (after Dineley, 1976).

The **body form of earlier agnathans** is remarkably simple, e.g. cyathaspids, several pteraspids, amphiaspids, psammosteids, and osteostracans. Attached to their stout armoured body, consisting of separate or fused elements, was a powerful tail with a prominent tail fin, the only instrument for propulsion in a scombroid swimming mode (according to the terminology of Kokshaysky, 1974). In *Drepanaspis* (Text-fig. 3A) the tail fin comprises more than 1/4 of the total length of the animal. In some cases there were protrusive rims along the sides of the trunk forming elementary keels. With time, the body shape became more complicated. As shown by Moy-Thomas and Miles (1971), the skeletal outgrowths, i.e. rigidly fixed lateral and dorsal spines or keels appeared to fulfil at least partly the function of paired and unpaired fins in fish. The body became slender, and a rostrum developed so that it could attain a higher swimming speed (Text-fig. 4). The extraordinary "horns" running anterolaterally from the front margin of the carapace in a new representative of the osteostracans (Early Devonian, Severnaya Zemlya) remain at present functionally unclear. High skeletogenous activity of the skin in fossil agnathans can also be exemplified by the healing of injuries. This is clearly seen in several specimens of psammosteid branchial and dorsal plates which completely healed after having been bitten into by predatory fishes (Mark-Kurik, 1966).

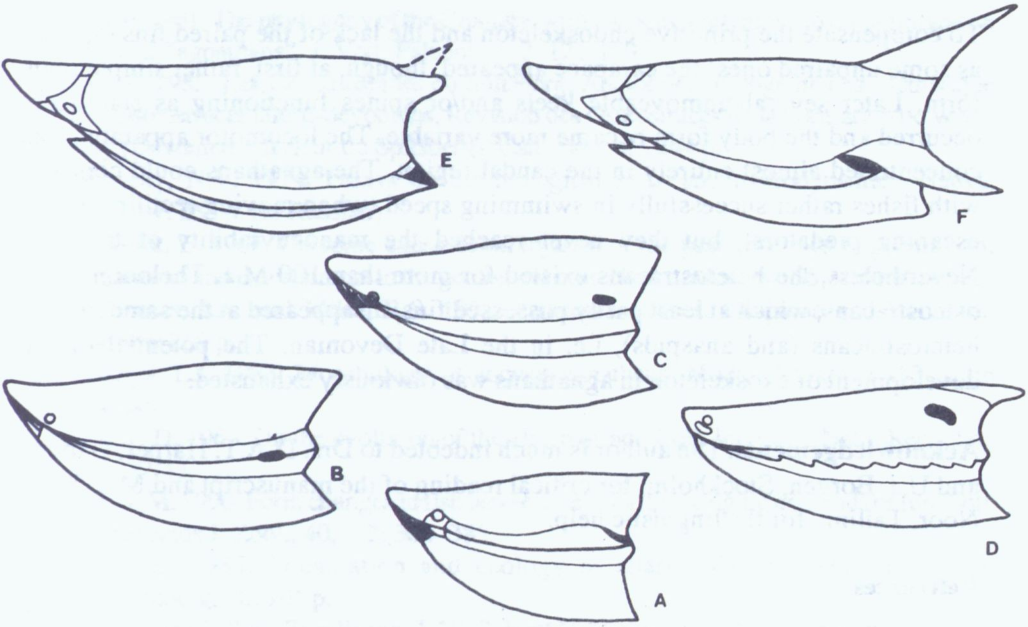
The **tails** of heterostracans and other agnathans have been considered specially in some papers, e.g. Denison, 1971 and Janvier, 1981. It must be emphasized that the preservation of heterostracan tails is much poorer in comparison with the carapaces of these animals. The tails, being extremely rare, are deformed and their delicate parts are lost. The remaining portions give an idea of the heterostracan tails as massive and insufficiently flexible, even as a short whip-like structure. The reconstructions of *Drepanaspis* (Gross, 1963), *Ctenaspis* (Dineley, 1976; Text-fig. 3B in this paper) and also *Athenaegis* (Soehn and Wilson, 1990) show that their tail fins were powerful instruments for swimming as well as for the avoidance of predators. In *Athenaegis* the separate "rays" reinforcing the middle part of the fin were probably connected by soft tissues as in *Ctenaspis* (see Dineley, 1976, Fig. 8). Otherwise the efficiency of the fin was much smaller. The traditional viewpoint on the poor swimming abilities of the early vertebrates is under revision. E.g. Belles-Isles (1987), comparing *Pteraspis* with the recent tuna, considers the heterostracan as a fast and stable swimmer with, however, a limited manoeuvrability. It is obvious that in rectilinear motion several agnathans could compete with fishes in swimming speed but even complicated carapaces with keels and/or spines could not compensate the set of paired and unpaired fins in fish.

One more point in the structure of the early vertebrates is significant. There was to be a **correlation between respiratory apparatus, body form and locomotion** as evidenced by the various size, shape and position of the branchial openings in heterostacans. Turbulent water emerging from the openings situated in some cases at the posterolateral corners of the carapace, in the other in front of them at different distances or at the very lateral edges (Text-fig. 5) was to influence differently the vertical and may be also horizontal movement of the body. According to Bendix-Almgreen (1986) the exhalant water stream coming out of branchial openings could have stabilizing and balancing functions similar to those provided by pectoral fins in fish. It is worth mentioning that to be more functional the respiratory apparatus enclosed in the armour might be supported either by an actively moving animal or by a moving environment. These aspects should be considered when evaluating the locomotion of the animals on one side and their living conditions on the other.

The exoskeleton of agnathans was undoubtedly perfectly adapted to fulfilment of functions of the organism. In most cases the carapaces were not heavy (contrary to a widely accepted conception; see e.g. Dineley, 1988). As indicated by Obruchev



Text-fig. 4. Selected Silurian and Early Devonian heterostracans (A-E) and osteostracans (F-J) showing the variety of body form: A - *Protopteraspis sartokia*, B - *Larnovaspis goujeti*, C - *Rhinopteraspis dunensis*, D - *Protaspis macgrewi*, E - *Unarkaspis schultzei*, F - *Tremataspis mammillata*, G - *Cephalaspis lyelli*, H - *Boreaspis rostrata*, I - *Hoelaspis angulata*, J - new genus from Severnaya Zemlya. Reconstructions are simplified. A-E - from Blieck, 1984; F - from Denison, 1951; G-I - from Janvier, 1985; J - preliminary reconstruction by E. Mark-Kurik. Scale bar 1 cm.



Text-fig. 5. Position of branchial opening in Early Devonian heterostracans: A -*Anglaspis*, B - amphilaspid, closely related to *Putoranaspis*, C - *Gerronaspis*, D - *Kureikaspis*, E - *Europrotaspis*, F - *Podolaspis* (simplified from Novitskaya, 1983).

(1967), in pteraspids the paper-thin carapace with large cancellae was not much heavier than the skin itself. The same is true about the cyathaspids and, in particular, amphiaspids. Their microstructure shows that carapaces contained a lot of space for soft tissues (Novitskaya, 1983 etc.). Even in the late heterostracans — psammosteids with a more compact exoskeleton — the armour was evidently not so heavy as to cause a negative buoyancy. One should take into consideration the relative thickness of the armour as compared to the size of the animal.

Summing up, it is worth to mention that teleost fishes in their ontogeny and prior to obtaining the habitual mode of swimming, undergo a larval stage characterized by a long, slender, extremely flexible body and anguilliform locomotion (described by Osse, 1990 and other authors). Two characters in the development of the 10-15 mm long larvae are of interest: a rapid growth of the pectoral fins compensating the yaw of the head, and the stiffening of the tail fin which resulted in the ossification of fin rays. The fish ontogeny thus seems to recapitulate the evolutionary pattern of the early vertebrates.

Under the influence of the vertebrate assemblages, existing evidently since the early Paleozoic and including predatory fishes, at least a part of the agnathans lost their slender worm- like body shape and anguilliform swimming mode. The comparatively short and stout body developed with a powerful tail attached to it.

To compensate the primitive endoskeleton and the lack of the paired fins (as well as some unpaired ones) the carapace appeared, though, at first, rather simple in its form. Later several unmoveable keels and/or spines functioning as stabilizers occurred and the body form became more variable. The locomotor apparatus was concentrated almost entirely in the caudal region. The agnathans could compete with fishes rather successfully in swimming speed (when moving rectilinearly or escaping predators), but they never reached the manoeuvrability of the fish. Nevertheless, the heterostracans existed for more than 100 M.a. Thelodonts and osteostracans, which at least partly possessed fins, disappeared at the same time as heterostracans (and anaspids), i.e. in the Late Devonian. The potential of the development of exoskeleton in agnathans was obviously exhausted.

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The modes of swimming of sarcopterygians

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Abstract. The sarcopterygians are here divided into 4 groups according to their general morphology (and their mode of swimming). The living representatives of these groups and the limited morphological variation during their geological history help us to reconstruct their mode of propulsion and their habits. The coelacanths probably used a combined slow and precise mode of propulsion with sudden dashes. Some alternating and synchronous movements of the paired, anal and second dorsal fins during the precision-swimming are pointed out in *Latimeria*. The same movements are used by some living fishes in the same swimming mode. The dipnoans must have used an anguilliform precise swimming mode since the late Devonian. They were probably also able to use an acceleration swimming mode for capturing prey. The fusiform rhipidistians (osteolepiforms sub-group I) were specialized in the acceleration swimming mode for quick dashes. Their habits must have resembled those of the living pike (*Esox*). The other rhipidistians (sub-group II) include generalist swimmers, and it is more difficult to deduce their habits.

Introduction

The study of hydrodynamics and functional anatomy permits us to partially reconstitute the mode of life and habits of fossil fishes. I have earlier deduced the swimming mode of the osteostracans and pteraspids (Belles-Isles, 1987). The habits of cornuate osteostracans must have resembled those of the living demersal sharks (e.g. *Scyliorhinus*), whereas the habits of pteraspids must have been more or less similar to those of the living tuna (a fast and stable swimmer but with a limited manoeuverability).

In this paper, I try to determine which swimming modes were used by the sarcopterygians from their morphological features, and I conclude that the swimming modes, like their morphology, have varied little during the evolutionary history of this group.

We must reject the conception that the primitive fishes were poor swimmers (Belles-Isles, 1987). The strange morphologies or the absent structures in some fossil groups do not signify that these fishes necessarily crawled along the bottom. They had certainly some adaptations to swimming or to their environment, even if we do not find any equivalent features among the living fishes. It would be wrong to say, for example, that a seahorse (*Hippocampus*), a slow but precise swimmer, swims badly; rather it has very special habits. The adaptations to swimming have no analogy with "primitiveness" or with phylogeny. Otherwise, with this argument, some aquatic insects would be more evolved than some fishes. This is nonsense. They have merely different adaptations for different ways of life.

Principles and definitions

We can define three swimming modes used by living fishes (there are some uncommon exceptions) and each one is characterized by specific morphological features. Unfortunately, the majority of fish use two or three modes, making their characteristic features less obvious. They are the "generalist or undefined swimmers". They exhibit morphological compromises and they are less effective in each swimming mode as compared to a "specialist swimmer", but they can live in various environments.

The three swimming modes are: 1) "acceleration swimming", 2) "maintained swimming", and 3) "manoeuverable swimming".

To move forward, a fish must overcome an opposing force called drag. It is mathematically defined (Webb, 1982) as:

$$D=M\cdot a+1/2p\cdot S\cdot V^2\cdot kC_D$$

where M is the mass of the fish, a is the acceleration, p is the density of the liquid, S is the surface area of the fish, V is the swimming speed, and kC_D is the drag coefficient (it takes into account the lateral body motions, the Reynold's number, the surface used, etc.) (Lighthill, 1975; Webb, 1975; Bone, 1977).

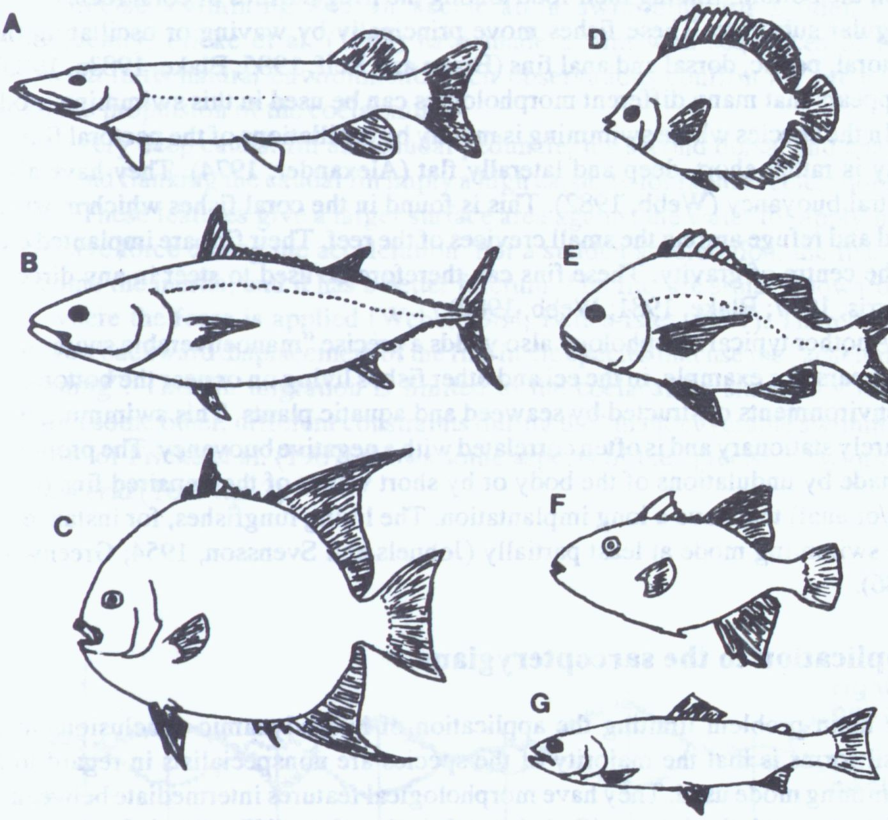
The first term of this equation is that due to inertia and the second is that due to friction. The magnitude of these two components differs between the "acceleration" and the "maintained" swimming. The differences in these components have distinct consequences for functional design.

"Acceleration swimming"

In this swimming mode, the first term of the preceding equation (M·a) is the most important, since during a sudden dash the acceleration is very high. The non-muscular mass which is not directly used to yield a thrust tends to reduce the forward acceleration (Webb, 1982; Gero, 1952). Thus, in the pike (Text- fig. 1A), which often uses quick accelerations for capturing a prey, as much as 60% of the body mass consists of paravertebral muscles. The other features of this swimming mode are the backward displacement of the centre of gravity, a deep caudal fin and caudal peduncle, the unpaired fins displaced backward, and a rather lengthened profile (Webb, 1975, 1984; Daniel, 1984; Gero, 1952; Belles-Isles, 1987).

"Maintained swimming"

This swimming mode is used by the Scombridae (Text-fig. 1B) and some sharks (Reif, 1981; Reif and Weishampel, 1986), which move at high and constant speed. Their swimming is continuous. Their acceleration is, hence, nearly zero and the drag equation is equivalent to $1/2\cdot p\cdot S\cdot V^2\cdot kC_D$. In the specialized fishes of this



Text-fig. 1. Outline drawings of teleosts illustrating three different specialist swimmers A, Pike (*Esox*), a specialist of the "acceleration swimming"; B, Tuna (*Thunnus*), a specialist of the "maintained swimming"; C to F, Specialists of the precise "Manoeuverable swimming" by oscillation of their paired fins, C, Spadefish (*Chaetodipterus faber*); D, Butterflyfish (*Chaetodon striatus*); E, Black Margate (*Anistotremus surinamensis*); F, Triggerfish (*Canthidermis maculatus*), note the 1st dorsal spined fin and the 2nd dorsal flexible fin; G, Rainbow trout (*Salmo gairdneri*), a generalist swimmer using the 3 swim-types.

swimming mode we notice the following features: the centre of gravity is approximately in the front third of the body, the caudal peduncle is very narrow, yet stiff, the caudal fin has a semi-lunar form, the paired fins are relatively small or retractable against the body, and the buoyancy is negative (Webb, 1975, 1982, 1984; Belles-Isles, 1987; Reif, 1981; Reif and Weishampel, 1986).

"Manoeuverable swimming"

Without doubt this swimming mode is the least understood and the least investigated (Webb, 1984; Blake, 1983a and b). It is used by fishes moving slowly in midwater or on the bottom, finding their food among the irregularities of coral reefs or other irregular substrate. These fishes move principally by waving or oscillating their pectoral, pelvic, dorsal and anal fins (Braun and Reif, 1985; Blake, 1983a, 1983b). It appears that many different morphologies can be used in this swimming mode.

In the species where swimming is mainly by oscillations of the pectoral fins, the body is rather short, deep and laterally flat (Alexander, 1974). They have also a neutral buoyancy (Webb, 1982). This is found in the coral fishes which must find food and refuge among the small crevices of the reef. Their fins are implanted close to the centre of gravity. These fins can therefore be used to steer in any direction (Harris, 1937; Blake, 1981; Webb, 1982).

Another typical morphology also yields a precise "manoeuverable swimming". It appears, for example, in the eel and other fishes living on or near the bottom, also in environments obstructed by seaweed and aquatic plants. This swimming mode is rarely stationary and is often correlated with a negative buoyancy. The propulsion is made by undulations of the body or by short waves of the unpaired fins (dorsal and/or anal) that have a long implantation. The living lungfishes, for instance, use this swimming mode at least partially (Johnels and Svensson, 1954; Greenwood, 1986).

Application to the sarcopterygians

The main problem limiting the application of hydrodynamic conclusions to the fossil forms is that the majority of the species are nonspecialists in regard to the swimming mode used. They have morphological features intermediate between the different morphologies specified above. It is therefore difficult to infer their mode of life. Nevertheless, the sarcopterygians are very interesting with regard to their swimming morphology because their subgroups (Dipnoi, osteolepiforms, porolepiforms, and especially the coelacanths) have been remarkably constant in their morphology during their geological history. Furthermore, there are some living representatives of this group permitting correlation and verification of the predictions. This stability in their morphology most probably indicates a constant mode of life during their history.

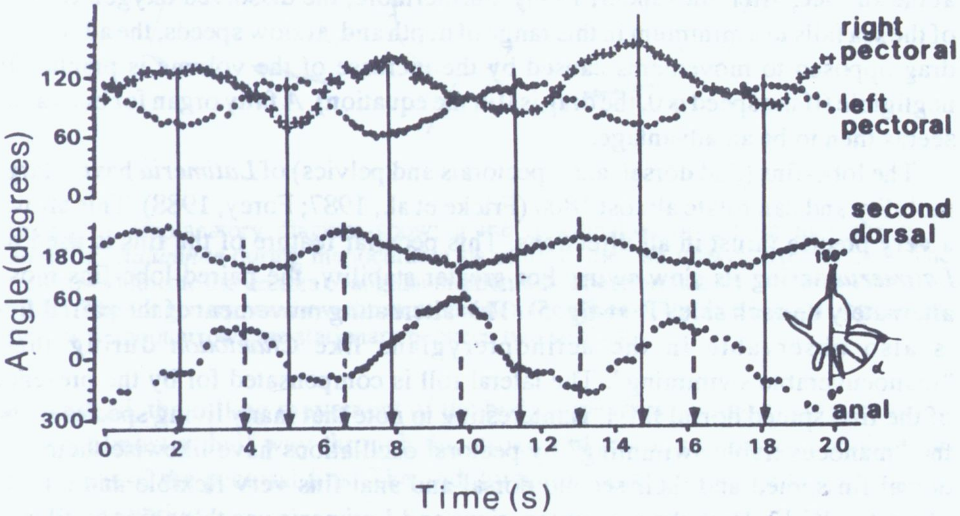
I have classified the sarcopterygians here into four groups. Even if I do not presume and do not discuss the phylogenetic relationships, this classification is in accord with recent ideas on this subject (with the exception of the porolepiforms, which is a paraphyletic group). The four groups are the coelacanths, the osteolepiforms (rhipidistians subgroup I), the other rhipidistians (subgroup II), and the dipnoans.

The coelacanths

I have earlier made some predictions about the swimming of the coelacanths (unpublished) according to their morphology and the principle of hydrodynamics.

I have determined that the coelacanths were adapted to two swimming modes: a slow precise swimming and an acceleration swimming for sudden starts. Subsequently, Fricke et al. (1987) have made a film with sequences of living *Latimeria* in its natural environment. Their observations confirm my predictions about the propulsion of the coelacanths.

The very deep caudal fin and caudal peduncle, the second dorsal and anal fins behind and flanking the caudal fin imply a high capacity for rapid accelerations and dashes. These features give a larger surface area against the water for applying the propulsive force during the acceleration. For a sudden acceleration, the fish must overcome the inertia, and it has a better fulcrum if its fins are situated towards the rear, where the force is applied (Webb, 1984; Belles-Isles, 1987). Therefore, we observe a backward displacement of the fins in the species that use the "acceleration swimming". This fin migration is limited to the coelacanths since they have to confront some other, different constraints during the "manoeuverable swimming". The film of Fricke et al. (1987) shows some aspects of the "precision swimming" in *Latimeria* (Text-fig. 2).



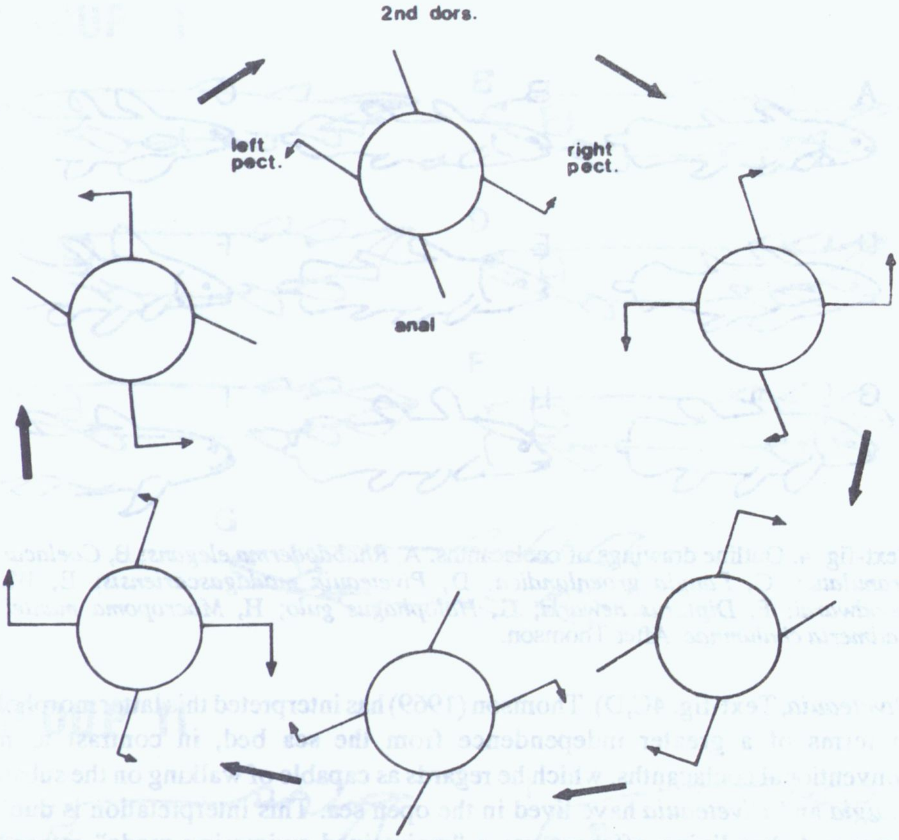
Text-fig. 2. Graph showing the fin coordination during the "manoeuverable swimming" of *Latimeria chalumnae*. The movements of the fins are indicated as the temporal variation in the angle between the fin axis and a vertical line through the center of gravity, the fish being seen from behind. The unbroken arrows indicate the times when the paired fins are at their maximal displacement, and the dotted arrows indicate the same for the 2nd dorsal and anal fins. The lateral and median fins are synchronized, but with a delay of a half beat. After Fricke et al.

Latimeria execute slow upward migrations nocturnally towards shoals (about 120 m depth), drifting with the currents. During this drifting, the stability of the swimming is ensured by alternate movements of the paired fins as well as by the 2nd dorsal and the anal fins. The neutral buoyancy and distribution of the fins around the center of gravity make these slow and precise movements easier.

The lung of *Latimeria* has been transformed into a fatty organ (Millot and Anthony, 1958) and may be used as a buoyancy organ. It is known that whenever fat is used to create a negative buoyancy, the drag is increased by about 20% as compared to the swimming of a non-fatty fish. This is because the incorporation of fats into the tissues increases the volume of the fish and offers more surface area which causes more drag (cf. equation) (Alexander, 1977). Apparently the swimbladder is more efficient and increases drag only by about 4% (Alexander, 1974, 1977), but it has a serious disadvantage. Its volume depends on the pressure, and hence on the depth, of the fish. There is only one depth at which the fish has neutral buoyancy. The process of adjustment by gas secretion or gas excretion tends to be slow. On the other hand, the fats have almost the same efficiency at every depth (Corner et al., 1969). In the deep water in which *Latimeria* lives, each small upward or downward displacement would require a great quantity of secretion or resorption of O_2 in the swimbladder (about 20 times more O_2 at 200 m depth than at the surface, after Alexander, 1974). Furthermore, the dissolved oxygen content of the sea falls to a minimum in this range of depth and, at slow speeds, the additional drag opposed to movements caused by the increase of the volume is practically negligible (if the speed is 0, the drag is 0 in the equation). A fatty organ for buoyancy seems then to be an advantage.

The lobe-fins (2nd dorsal, anal, pectorals and pelvics) of *Latimeria* have a large mobility and can rotate almost 1800 (Fricke et al., 1987; Forey, 1988). This allows a very precise thrust in all directions. This peculiar feature of the fins is used by *Latimeria* during its slow swim. For greater stability, the paired lobe-fins move alternately on each side (Text-fig. 5). This alternating movement of the paired fins is also observable in the actinopterygians like *Chaetodon* during their "manoeuverable swimming". The lateral roll is compensated for by the presence of the first spined dorsal fin. It is interesting to note that many living species using the "manoeuverable swimming" by pectoral oscillations have likewise their first dorsal fin spined and their second dorsal and anal fins very flexible and mobile (Text-fig. 1C-F). Both the actinopterygians and *Latimeria* use these fins similarly.

It seems that the 2nd dorsal and the anal fins take part in stabilizing the lateral roll. They move synchronously towards opposite sides to prevent rolling generated by the pectoral fins (Text-figs. 2,3) but with a delay of one half beat behind the latter. For instance, when the right pectoral fin finishes its upward movement (and the left one its downward movement at the same time), the body would acquire a clockwise rolling movement (seen from behind) if the anal and the 2nd dorsal fins did not make a compensating displacement in the opposite direction with a delay. This half beat delay permits a more efficient action of the 2nd dorsal and the anal

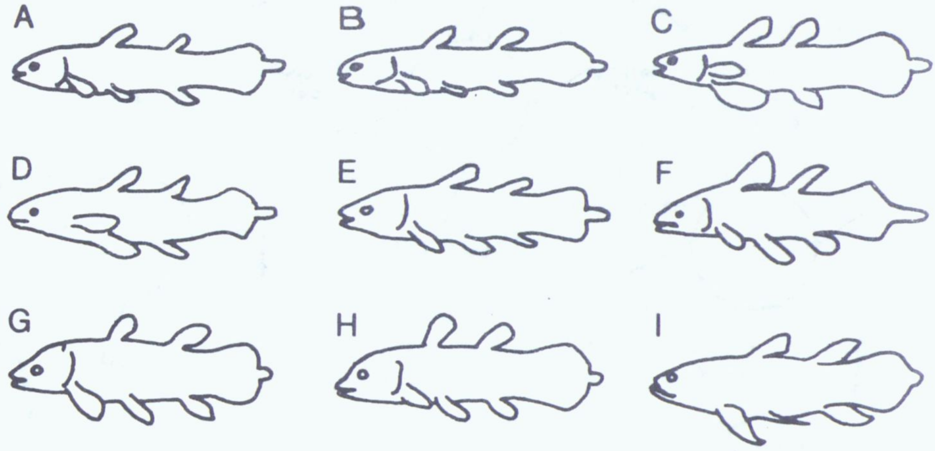


Text-fig. 3. Explanatory diagram showing the coordination of the fin movements in *Latimeria chalumnae* during manoeurable swimming, the fish viewed from behind. The fine arrows indicate the vectors of angular momentum. The short fine arrows show the initial motion. The longer arrows show the motion when the speed of the fins is at the maximum. The fins without arrows are stationary between two strokes.

fins. Indeed, the rolling movement of the body appears when the pectoral fins are already almost at half way through the stroke and continues after the end of the movement of the pectoral fins. The 2nd dorsal and anal fins move very precisely during this period.

The calculated torque of the lobe-fins indicates equal and opposed forces for the paired fins with the unpaired lobe-fins (2nd dorsal + anal) during all phases of the oscillation. It is nevertheless a very rough measure because the position of the centre of gravity and the mass of the fish are only estimated.

I have observed the same synchronization of the fins in many living teleosts swimming steadily in an aquarium. Some species of coelacanths have their pectoral fins implanted more laterally than in *Latimeria*, and their pelvic fins have a thoracic insertion under the pectoral girdle, in front of the level of the first dorsal fin (*Laugia*,



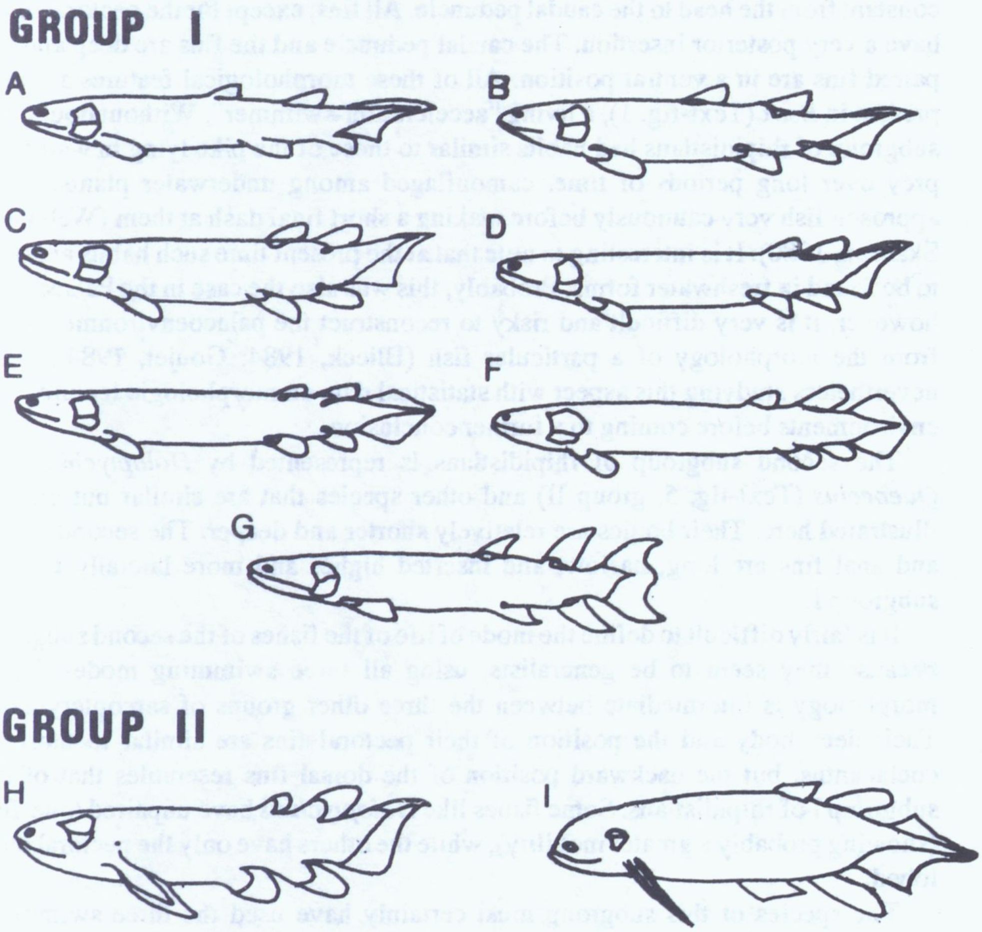
Text-fig. 4. Outline drawings of coelacanths. A, *Rhabdoderma elegans*; B, *Coelacanthus granulatus*; C, *Laugia groenlandica*; D, *Piveteauia madagascariensis*; E, *Whiteia woodwardi*; F, *Diplurus newarki*; G, *Holophagus gulo*; H, *Macropoma mantelli*; I, *Latimeria chalumnae*. After Thomson.

Piveteauia, Text-fig. 4C,D). Thomson (1969) has interpreted this latter morphology in terms of a greater independence from the sea bed, in contrast to more conventional coelacanths, which he regards as capable of walking on the substrate. *Laugia* and *Piveteauia* have lived in the open sea. This interpretation is dubious, because fishes living offshore use a "maintained swimming mode" rather than "manoeuverable swimming", and the walking movements of the fins are demonstrated falsely (Fricke et al., 1987). Probably, they were more adapted to a rocky reef environment, whereas the other coelacanths, like *Latimeria*, were rather more adapted to a deepwater environment, near the bottom.

Rhipidistians

The morphology of some subgroups of rhipidistian fishes is relatively conservative, yet does not reflect the polyphyletism of the group. It is just a question of general external morphology reflecting an approximately similar mode of life. I have divided the rhipidistians into two subgroups according to whether the different species are more or less adapted to ambush hunting (like the living pike *Esox*, Text-fig. 5; group I reassembling mainly the ostelepiforms) or to a combined generalist swimming (Text-fig. 5; group II reassembling the rest of the rhipidistians).

First, it seems that the form of the caudal fin (heterocercal or homocercal) is not as important for propulsion as the position of the other fins (Webb and Smith, 1980). They have demonstrated, with different amputations of the fins in living fishes, that the performance during the "maintained swimming" and the "acceleration



Text-fig. 5. Outline drawings of rhipidistians. A, *Osteolepis panderi*; B, *Osteolepis macrolepidotus*; C, *Thursius macrolepidotus*; D, *Thursius pholidotus*; E, *Gyroptychius agassizi*; F, *Glyptopomus kinnairdi*; G, *Eusthenopteron foordi*; H, *Holoptychius* sp.; I, *Qebecius quebecensis*. After Thomson, and Schultze and Arsenault.

swimming" are not too much changed with a heterocercal fin (90-92% efficiency with a heterocercal fin, and 0-73% without anal and/or dorsal fins). Furthermore, the thrust produced by a heterocercal fin crossed always the centre of gravity for every angle of the notochordal axis. All heterocercal caudal fins have the same type of thrust (Thomson and Simanek, 1976). It is not surprising therefore to find a caudal fin heterocercal like that in *Thursius* or *Osteolepis* (Text-fig. 5) in the same group as a homocercal caudal fin like that in *Eusthenopteron*. In this group, the overall morphologies are very similar.

The first subgroup of rhipidistians (Text-fig. 5, group I) includes the more fusiform forms. The body is very streamlined, narrow, and its height is relatively constant from the head to the caudal peduncle. All fins, except for the pectoral ones, have a very posterior insertion. The caudal peduncle and the fins are deep and the paired fins are in a ventral position. All of these morphological features are also present in *Esox* (Text-fig. 1), a living "acceleration-swimmer". Without doubt this subgroup of rhipidistians had habits similar to those of the pike lying in wait for a prey over long periods of time, camouflaged among underwater plants. They approach fish very cautiously before making a short final dash at them (Webb and Skadsen, 1980). It is interesting to note that at the present time such habits are only to be found in freshwater forms. Probably, this was also the case in the Palaeozoic; however, it is very difficult and risky to reconstruct the palaeoenvironment only from the morphology of a particular fish (Blieck, 1984; Goujet, 1984). I am nevertheless studying this aspect with statistical data on morphologic features and environments before coming to a further conclusion.

The second subgroup of rhipidistians is represented by *Holoptychius* and *Quebecius* (Text-fig. 5, group II) and other species that are similar but are not illustrated here. Their bodies are relatively shorter and deeper. The second dorsal and anal fins are long, narrow, and inserted higher and more laterally than in subgroup I.

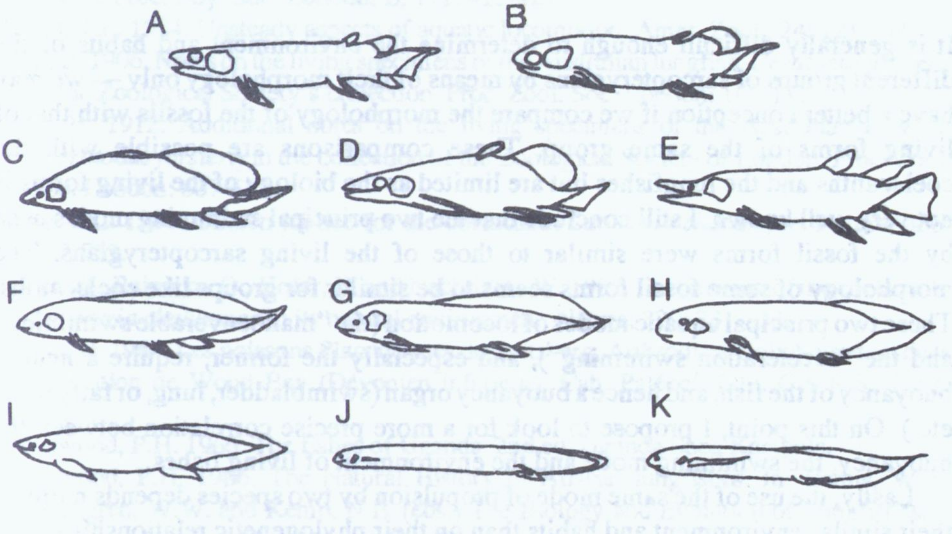
It is fairly difficult to define the mode of life of the fishes of the second subgroup because they seem to be generalists, using all three swimming modes. Their morphology is intermediate between the three other groups of sarcopterygians. Their deep body and the position of their pectoral fins are similar to those of coelacanths, but the backward position of the dorsal fins resembles that of the subgroup I of rhipidistians. Some fishes like *Holoptychius* have unpaired lobe-fins (showing probably a greater mobility), while the others have only the pectoral ones lobed.

The species of this subgroup must certainly have used the three swimming modes to different degrees, according to their different morphologies. Such "generalist swimmers" could have lived in many different environments and it is almost impossible to deduce their mode of life.

Dipnoans

The morphology of the lungfishes seems relatively diverse in their early history (Martin, 1987), being adapted to many different swimming modes (precise and/or acceleration swimming; see *Dipterus*, *Scaumenacia* and *Rhynchodipterus* (Text-fig. 6). The morphology seems to have remained more constant since the late Devonian (e.g. *Phaneropleuron*), being more eel-like up to the present.

Scaumenacia and *Fleurentia* have a morphology closest to those of the reef manoeuvring fishes with the very movable pectoral fins, the laterally flattened body and the 2nd dorsal and anal fins visibly very flexible and mobile. However the longer body and the position of the large 2nd dorsal fin, the general insertion of the



Text-fig. 6. Outline drawings of dipnoans. A, *Dipterus valenciennesi*; B, *Pentlandia macroptera*; C, *Scaumenacia curta*; D, *Fleurentia denticulata*; E, *Rhynchodipterus elginensis*; F, *Phaneuropleuron andersoni*; G, *Uronemus lobatus*; H, *Conchopoma gadiforme*; I, *Neoceratodus forsteri*; J, *Lepidosiren paradoxa*; K, *Protopterus annectens*. After Thomson.

fins in the rear part of the body, and the maximal height of the body at the level of the propulsive part show their obvious capacity for acceleration swimming.

These fishes must have lived concealed among rocks or plants until an unwary prey came near enough to be captured by a short dash. They probably looked for their food in places inaccessible to fish with other swimming modes, for instance in cervices in reefs, like the living *Chaetodon*. For this purpose, *Scaumenacia* must have had a neutral buoyancy and might have used its lungs as a buoyancy organ (Thomson, 1969). Either it would gulp air at the surface or its lungs were to be modified into a special, as yet unknown flotation organ.

The more recent fossil forms probably had habits similar to those of the living forms. Unfortunately, the biology of the living lungfishes is not very well known (Greenwood, 1986; Kemp, 1986) and the correlations are difficult. Nevertheless it seems that they spend the majority of their life on the bottom of pools and marshes, feeding on plants debris, invertebrates and small fishes (Illidge, 1894; Longman, 1928; Carter and Beadle, 1930; Greenwood, 1966; Thomson, 1969). They use eel-like swimming (Johnels and Svensson, 1954; Rosen et al., 1981) for moving among aquatic plants (Dean, 1906, 1912). However, as lungfishes are active mainly during the night (Grigg, 1965) and have therefore been little observed, it is possible that they can also make dashes to capture small fishes (Ramsay, 1876), but we need further observations concerning about these last presumptions.

Conclusions

It is generally difficult enough to determine the environment and habits of the different groups of sarcopterygians by means of their morphology only — we may have a better conception if we compare the morphology of the fossils with that of living forms of the same group. These comparisons are possible with the coelacanths and the lungfishes but are limited as the biology of the living forms is not very well known. I still conclude that the two principal swimming modes used by the fossil forms were similar to those of the living sarcopterygians. The morphology of some fossil forms seems to be similar for groups like coelacanths. These two principal aquatic modes of locomotion (the "manoeuverable swimming" and the "acceleration swimming"), and especially the former, require a neutral buoyancy of the fish, and hence a buoyancy organ (swimbladder, lung, or fatty liver, etc.). On this point, I propose to look for a more precise correlation between the buoyancy, the swimming mode and the environment of living fishes.

Lastly, the use of the same mode of propulsion by two species depends more on their similar environment and habits than on their phylogenetic relationships.

Acknowledgements. This research was financially supported by an Alexander von Humboldt-Stiftung Grant.

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The locomotor apparatus of *Panderichthys rhombolepis* (Gross), a supplement to the problem of fish-tetrapod transition

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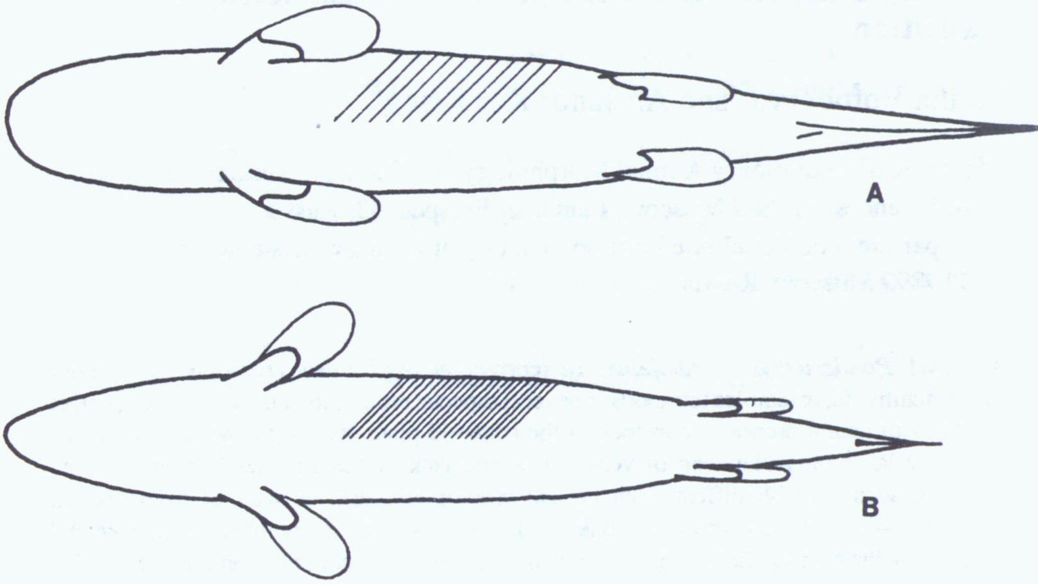
Abstract. *Panderichthys rhombolepis*, the representative of a new crossopterygian order Panderichthyida, resembles tetrapods in several aspects: reduction of unpaired fins, contact of ribs with neural arches, occurrence of the coracoid plate, its contact with the clavicle, relatively large muscular lobe of ventral fins and lack of basal scutes in fins. In some characteristics the fish differs from typical crossopterygians, as well as from ancient tetrapods — its tail is too short, its trunk is relatively long and the number of endoskeletal elements in the pectoral fin is reduced. Considering all these peculiarities and reconstruction of the body form, as well as flexibility of the trunk, orientation of the pectoral fin and mobility of the shoulder joint, the fish is supposed to have used the primitive type of terrestrial locomotion: its paired fins only "anchored" first the anterior and then the posterior ends to the substratum, while its loose end moved forward by means of lateral bending of the trunk. One modern fish species uses the same way of locomotion. P. rhombolepis evidently could hunt on the littoral during the ebb, searching for the prey in water with the aid of its elevated eyes; it could also crawl from one pool into another during the shallowing of the lagoon.

The recently defined crossopterygian order Panderichthyida Vorobyeva (in press) is of special interest for the solving of the problem of terrestrial vertebrates origin. This order is treated as a sister group of tetrapods. It includes the Late Devonian *Elpistostege* from Eastern Canada (Schultze, Arsenault, 1985) and Devonian panderichthyids from the USSR, at present ascribed to the genus *Panderichthys* (Vorobyeva, 1962; Vorobyeva, Obruchev, 1964; Vorobyeva, Lyarskaya, 1968). The remains of the type species Panderichthys rhombolepis (Gross, 1930) are the most complete. Considerable additional information on this species was received in the 70s after the discovery of the burial-site at Lode (Latvia), where almost complete skeletons were uncovered together with other fossil fishes and plant remains (Lyarskaya, 1981).

Five specimens of *Panderichthys rhombolepis* with postcranial skeletal parts preserved were examined: (1) an almost complete but the smallest individual (body length about 90 cm) from the collection of the Nature Museum of Latvia (not yet numbered); (2) no 3547/19 from the Palaeontological Institute (PIN) Russian Acad. Sci. collection, a larger individual with the tail part missing;



Text-fig. 1. Reconstructions of *Osteolepis macrolepidota* (A) (from Jarvik, 1948, simplified) and of *Panderichthys rhombolepis* (B), in ventral view, both are reduced to equal head length. Hatching shows the scale rows.

(3) no Pi 1633* from the Institute of Geology, Acad. Sci. Estonia collection, an even larger individual, the tail part missing; (4) PIN coll. no 3547/18, a large individual, represented only by the head and the pectoral part of the trunk; (5) PIN coll. no 3547/26, the largest individual (calculated body length up to 150 cm), the tail part missing.

A new reconstruction of the body shape in *Panderichthys rhombolepis* (Text-fig. 1B) was made on the basis of a series of measurements and using Jarvik's (1948) cross sections of *Osteolepis macrolepidota*.

The present account deals with the biomechanical analysis of the locomotor apparatus in *Panderichthys rhombolepis*, which enabled to put forward a hypothesis on the locomotion specialization and biology of this fish.

Postcranial skeleton morphology

Panderichthys rhombolepis features about 50 trunk **vertebrae**. Their bodies are, unlike those in other crossopterygians, formed exclusively by intercentra, while

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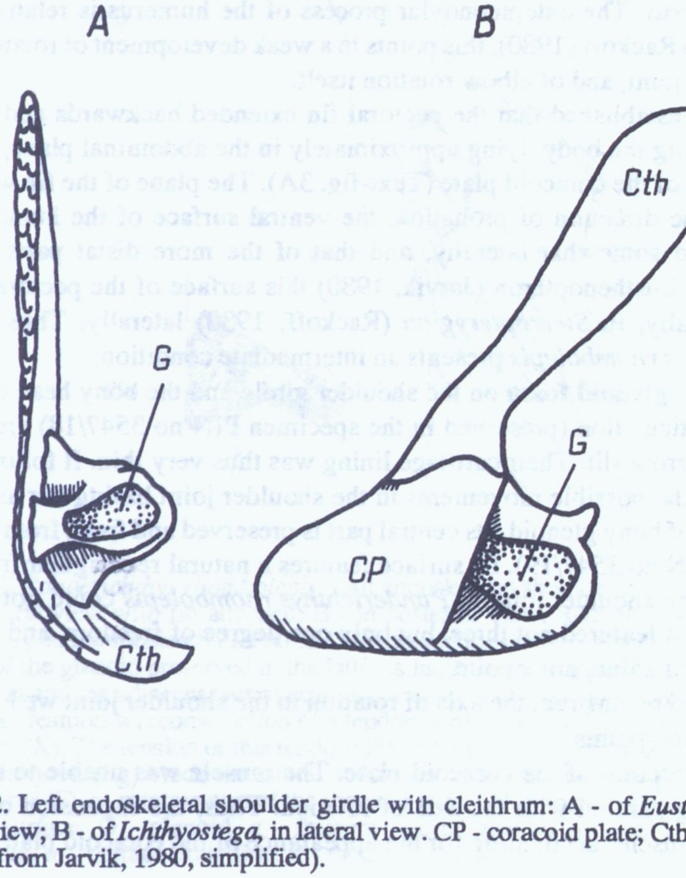
* This number was erroneously applied to quite another specimen (belonging to the other species, the other locality and the other collection) in Vorobyeva, 1987 (Pl. VIII, fig.3.) Now that specimen is numbered as PIN no 1737/57 (remark of the editor).

the pleurocentra are missing; each intercentrum has a suture connection with the base of neural arch posterior to it (Vorobyeva, Tsessarsky, 1986).

The arising resegmentated state of the vertebrae can be accounted for by the nature of rib articulation (Shishkin, 1987). All of the trunk vertebrae feature rather long, strong, dorso-ventrally flattened and horizontally orientated ribs. Each rib is fused with the intercentrum and has a suture connection with the base of the neural arch. The latter connection can be treated as a derived condition: among the crossopterygians it is shared only by *Eusthenopteron* (Andrews, Westoll, 1970), while in tetrapods it is typically present. However, in *Panderichthys rhombolepis* the double articulation of the rib is not subdivided into separate heads. Nevertheless, long, wide and rigidly attached ribs could reinforce the trunk in a manner described for the bicipital ribs (Schmalhausen, 1964). This fact suggests the possible of adaptation of *Panderichthys rhombolepis* to the terrestrial environment, further supported by the reduction of median fins (at least the anterior dorsal one is absent) and a relatively large size of the pelvic fin lobe (Text-fig.1).

Unlike other crossopterygians, the **endoskeletal shoulder girdle** is represented not by the "tripod" structure (Text-fig. 2A), but mainly by an extensive coracoid



Text-fig. 2. Left endoskeletal shoulder girdle with cleithrum: A - of *Eusthenopteron*, in posterior view; B - of *Ichthyostega*, in lateral view. CP - coracoid plate; Cth - cleithrum; G - glenoid (from Jarvik, 1980, simplified).

plate lying in the abdominal plane, and being attached not only to the cleithrum, but to the clavicle as well (Text-fig. 3A, clavicle removed). The plate is roughly similar to that of *Ichthyostega* (Text-fig. 2B). However, in *Ichthyostega*, as in other primitive tetrapods, the glenoid fossa occurs on the lateral side of the endoskeletal girdle, anterior to its caudal margin, and faces almost sideways, while in *Panderichthys rhombolepis* it occupies the posterior margin and faces almost backwards, as in other crossopterygians (cf. Text-fig. 2A, 3B). The appearance of the coracoid plate was, probably, caused by the expansion of proximal ventral limb muscles.

The number of endoskeletal elements in crossopterygian **pectoral fins** is lower than in the tetrapod fore limbs (*Sauripterus*, exceptionally, has more rays than ever observed in tetrapods; see Thomson, 1968). Notably, among the crossopterygians *Panderichthys rhombolepis* features the lowest number of such elements (Text-fig. 3A). Apart from humerus, radius, ulna and intermedium, there is but a single element positioned postaxially to the intermedium (Worobjewa, 1975; Hinchliffe, Vorobyeva, 1989). All those elements of the pectoral fin are tightly packed and apparently performed as one single whole. The "wrist joint" was blocked by radius, which happened to be longer than ulna, like in *Eusthenopteron*, *Sterropterygion* and *Sauripterus*. The entepicondylar process of the humerus is relatively small. According to Rackoff (1980), this points to a weak development of rotators serving as the elbow joint, and of elbow rotation itself.

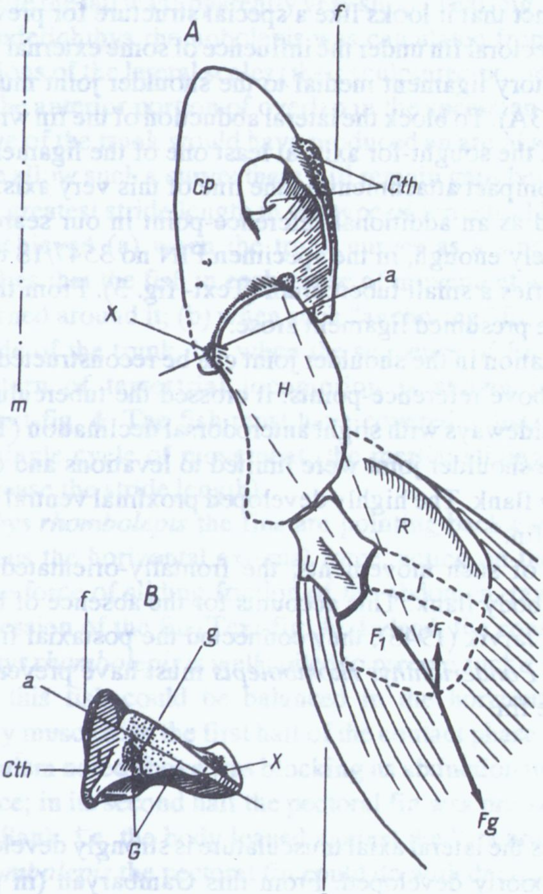
We have established that the pectoral fin extended backwards and somewhat sideways along the body, lying approximately in the abdominal plane, as a direct continuation of the coracoid plate (Text-fig. 3A). The plane of the fin was slightly twisted in the direction of pronation, the ventral surface of the humerus facing ventrally and somewhat laterally, and that of the more distal parts of the fin ventrally. In Eusthenopteron (Jarvik, 1980) this surface of the pectoral fin faces ventro-medially, in *Sterropterygion* (Rackoff, 1980) laterally. Thus the fin of *Panderichthys rhombolepis* presents an intermediate condition.

The bony **glenoid fossa** on the shoulder girdle and the bony head of humerus in natural articulation (preserved in the specimen PIN no 3547/18) are separated only by a narrow slit. Their cartilage lining was thus very thin. It follows that we can discuss the possible movements in the shoulder joint basing our assumptions on the form of bony glenoid (its central part is preserved and freed from rock in the specimen PIN no 3547/19). Its surface features a natural rectangular fracture (see below), so the shoulder joint in *Panderichthys rhombolepis* could not have been spherical — it featured not three, but only one degree of freedom, and its rotation axis presented a line, not a point.

In order to reconstruct the axis of rotation in the shoulder joint we have chosen three reference-points:

1. The direction of the coracoid plate. The muscle was unable to operate the joint, pulling parallel with the axis of rotation. Thus, the expansion of proximal ventral fin muscles accounting for the appearance of the coracoid plate must have

occurred more or less perpendicularly to the rotation axis of the shoulder joint. Correspondingly, the coracoid plate itself must have been directed roughly perpendicular to this axis. The new contact of the scapulocoracoid with the clavicle indicates the anterior growth of the coracoid plate.



Text-fig. 3. ***Panderichthys rhombolepis*****. Left endoskeletal shoulder girdle with cleithrum: A - in ventral view with fin attached; B - in posterior view. Reconstruction of the fin is based mainly on the specimen PIN no 3547/18, that of the girdle mainly on PIN no 3547/19. The part of the glenoid preserved in the latter is indicated by stipple; the area of the break of cleithrum and the adjacent part of scapulocoracoid in this specimen by regular hatching in "B". "A" features a reconstruction of a tendon, which, probably, arose from the "axial" tuberculum (X). The tension of this tendon (Fl) and the pressing of the articular surfaces in the shoulder joint (Fg) block the lateral abduction of the fin apt to be produced by some external force (F). a - rotation axis of the shoulder joint, CP - coracoid plate, Cth - cleithrum, f - flank surface, G - glenoid, g - fracture line of glenoid surface, H - humerus, I - intermedium, m - median body line, R - radius, U - ulna.**

2. Fracture line in the surface of the shoulder joint. The glenoid features a natural rectangular fracture; fracture line is almost vertical (Text-fig. 3B). The axis of rotation must have been perpendicular to this line, i.e. almost horizontal. Thus in the pectoral fin of *Panderichthys rhombolepis* lateral abduction was impossible. This conclusion is also evidenced by the fact that the posterior border of the cleithrum clearly formed a flange lateral to the glenoid (Text-fig. 3A).

3. Tuberculum on the endoskeletal shoulder girdle. The fracture of the glenoid surface is so distinct that it looks like a special structure for preventing the lateral abduction of the pectoral fin under the influence of some external force (see below). If so, a compensatory ligament medial to the shoulder joint must have also been present (Text-fig. 3A). To block the lateral abduction of the fin without interference in rotation around the sought-for axis, at least one of the ligament's endings must have featured a compact attachment on the line of this very axis. Such attachment could have served as an additional reference-point in our search for the axis of rotation. Fortunately enough, in the specimen PIN no 3547/18 the medial margin of the glenoid carries a small tuberculum (Text- fig. 3). From this tuberculum, in all probability, the presumed ligament arose.

The axis of rotation in the shoulder joint can be reconstructed with certainty on the basis of the above reference-points: it crossed the tuberculum just described, and further went sideways with slight anterodorsal declination (Text-fig. 3). So the movements in the shoulder joint were limited to levations and depressions of the fin along the body flank. The highly developed proximal ventral muscles served as depressors of the fin.

In the course of such movements, the frontally-orientated pectoral fin was sliding along the body flank. This accounts for the absence of basal scutes in the fin. According to Jarvik (1948), they connected the postaxial fin margin with the body wall and in *Panderichthys rhombolepis* must have prevented levations and depressions of the fin.

Locomotion

In all typical fishes the lateral axial musculature is strongly developed, while paired fin muscles are poorly developed. From this Gambaryan (in press) proposed a hypothesis on biomechanics of the earliest type of quadrupedal terrestrial locomotion: this must have employed paired extremities with minimal participation of their muscles. The forces applied to extremities must have been transferred mostly via their passive structures - skeletal elements and ligaments. Thus, the functions of extremities must have been restricted to subsequent "anchoring" of the anterior and then of posterior body ends on the substratum. Progression must have been achieved as follows: the hind end was dragged forward due to bending of the trunk, while the anterior end was "anchored"; then the anterior end was pushed forward due to straightening of the trunk, while the posterior end was "anchored".

The extremity is usually fixed on the ground by pressing to and, on the soft substratum, by pressing in. The pressing of the extremity is performed by its depressors. Indeed, these muscles were relatively highly developed in the pectoral fin of *Panderichthys rhombolepis*, judging by the size of its coracoid plate.

In the described type of locomotion the stride length greatly depends on the length and flexibility of the trunk; the tail does not participate in progression and presents an unwanted ballast. Indeed, the trunk in *Panderichthys rhombolepis* was relatively long, while the tail was apparently very short (Text- fig. 1). The flexibility of the trunk in Panderichthys rhomobolepis was calculated from its length, mean width and proportions of the lateral scales (their sculptured portion being about 3.5 times wider than the anterior portion of overlap in the specimen PIN no 3547/18). The strongest curve of the trunk would have produced an arc of about 60. The ribs, though wide, quite allow such a curve: there still remain gaps between them on the concave side. The greatest stride length in the type of terrestrial locomotion under consideration is achieved (a) when the trunk curves as a single arc, and not a sinusoid; this implies that the fish in each phase of movement was "anchored" by a single fin and turned around it; (b) when such "anchoring" fin was always found on the concave side of the trunk, i.e. when the sequence of fin involvement was lateral. This pattern of terrestrial locomotion is shown for *Panderichthys rhombolepis* in Text-fig. 4 The fish must have covered a distance of almost the head length in a single cycle of movement (the inertial sliding after each thrust would further increase the stride length).

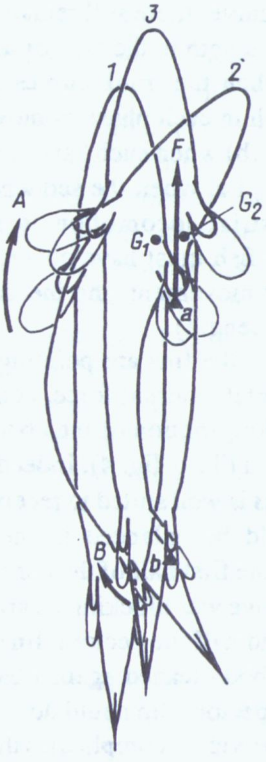
In *Panderichthys rhombolepis* the fins are pointing backwards while running along the body, thus the horizontal external force, acting on the "anchoring" fin which balances the force of sliding friction of the abdomen, must have produced lengthwise compression of the fin (Text-fig. 4). Indeed, the consolidated pectoral fin of *Panderichthys rhombolepis* is well suited to receive such a compression. The shoulder joint in this fish could be balanced in the horizontal plane without participation of any muscles: in the first half of the contact phase of the pectoral fin the passive mechanism noted above was blocking its abduction under the influence of the external force; in its second half the pectoral fin was pressed by the external force to the body flank, i.e. the body leaned against the "anchoring" fin. Thus, in *Panderichthys rhombolepis* the pectoral fin could do with depressor muscles only. Insufficient information on the pelvic fin complicates the discussion of it at present, but the relatively large lobe of this fin and the short tail of the fish suggest its terrestrial locomotion as shown in Text-fig. 4.

The described type of terrestrial locomotion is used nowadays by the teleost *Clarias batrachus* reaching 60 cm in length (it can be judged from the series of photographs, published in 1970 in the paper "Catfish walks on land", America, 161: 8-9; in Russian). However, this fish uses for "anchoring" the anterior lepidotrichial spine instead of the the pectoral fin lobe reduced in teleosts, and the tail instead of the pelvic fins.

Biology

The uncovered locomotory abilities of *Panderichthys rhombolepis* together with the burial type at Lode locality, allow to put forward some assumptions as to the habit of life of this predatory fish.

From the excellent preservation state of fossils in Lode (sporangia of *Archaeopteris* among them), it can be concluded that the organisms died, and consequently lived near their burial site. The latter apparently represented a freshened sea lagoon (see also Kuršs, this volume). *Panderichthys rhombolepis* could hunt on the littoral during the ebb, attacking the aquatic animals accidentally



Text-fig. 4. Reconstruction of the half of the locomotory cycle in Panderichthys rhombolepis (fish shown in ventral view to demonstrate fin bases). 1 - The trunk in straightened position. 2 - It is bent to the left side to the extreme while "anchored" by the left pectoral fin (marked by a black triangle a). The body has turned around on this fin (the direction is indicated by an arrow A), while the posterior part of the body has been dragged forward. The approximate direction of the horizontal component of the ground reaction is shown (F). In position 1, it passes to the lateral of the shoulder joint (point G1); in position 2 - to the medial of it (G2). 3 - The trunk has straightened once more, "anchored" by the left pelvic fin (black triangle b), while turning around on it (arrow B); the anterior part of the body has been pushed forward. In the next stage of the cycle the trunk bends to the right side.

left helpless on land. With the aid of its peculiar elevated eyes it could effectively search for them, swimming along the coast.

Furthermore, the Lode locality includes several lenses at a distance of 100-300 m one from the other, each including a series of fossil-bearing strata; probably such a pattern resulted from the periodic shallowing of the lagoon, which led to the isolation of small pools. *Panderichthys rhombolepis* could crawl from one pool into another in search for prey.

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The function of the cosmine pore canal system

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Abstract. The function of the pore canal system of cosmine is reanalyzed on the basis of previously published information, including the recent observations by the author that superficial resorption spread from the pore canal openings. The frequently suggested view that this system is a sensory, probably an electrosensory system, is considered unlikely. Instead it is suggested that the pore canal system, including the cavities, mainly contains a vascular plexus. Possibly the pore canal cavities may be specialized parts of this plexus, functioning as a reservoir for progenitor cells of scleroclasts.

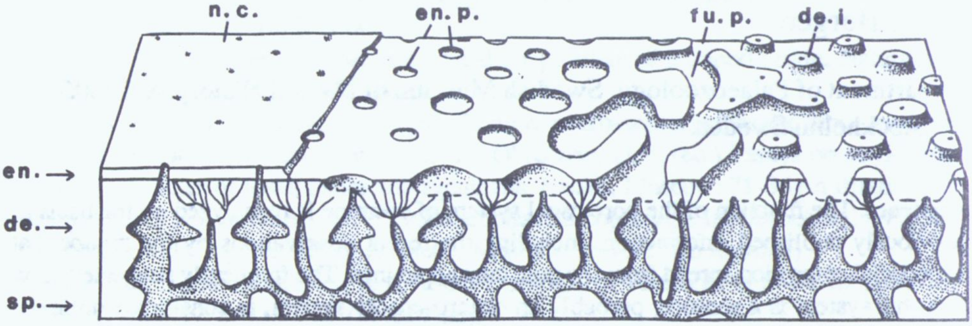
Cosmine can be briefly defined as a tissue combination covering external dermal bones, consisting from the outside of enameloid, dentine, and a thin layer of vascular bone (the so called spongiosa), where both dentine and enameloid are penetrated by a pore canal system that is continuous with the vascular canals of the spongiosa. The importance of the understanding of cosmine is due to its apparent occurrence in several groups of early vertebrates. Since no structures corresponding to cosmine exist among living animals, the only way to understand it is probably to describe as many structures and modifications of cosmine as possible, and to find interpretations that cover all these different configurations.

In a recent work (Borgen,1989) I studied some superficial, presumed resorption structures on three osteolepid lower jaws. The results of this paper are relevant to the interpretation of the function of the pore canal system. The function of this system is a central problem in the understanding of the biology of cosmine, and thus, also of the biology of early fishes. This paper is an attempt to interpret the function of the pore canal system, based on previously published observations by other authors, and on new information presented in Borgen (1989). In doing this I tentatively challenge some of the current views concerning cosmine biology.

Since important to some of the later discussions, I will first review relevant information from Borgen (1989):

(1) Resorption is seen to spread from the external openings of the pore canal system. Thomson (1977, p. 251) stated that resorption started with an enlargement of pores, but he could not determine which pores. In my material, this could be determined, as all three specimens showed a gradual transition from normal cosmine pore canal pores to expanded ones (exp.p., Text-fig. 1).

(2) In addition to normal cosmine and enlarged pore canal pores, there was one configuration in which the cosmineless areas around the pores had fused (fu.p., Text-fig. 1), leaving small dentine islets (de.i., Text-fig. 1), and one configuration in which cosmine was altogether absent. On one jaw, the distributions of the



Text-fig. 1. A schematic reconstruction of the observed stages of the superficial resorption process. Abbreviations; de., dentine; de.i., dentine islets; en.p., enlarged cosmine pores; en., enameloid; fu.p., enlarged pores in the process of fusing; n.c., normal cosmine; sp., spongiosa (vascular bone). Interrupted lines at the base of the areas under resorption indicates that the depth of these areas is unknown due to lack of sections.

different configurations were mapped. The configurations with normal cosmine (n.c., Text-fig. 1), expanded pores, and fused pores grade into each other, and have distributions suggesting a gradual process of resorption that spreads from a few sites on the jaw (four on the anterior half of the jaw).

(3) The distribution of areas of complete resorption did not fit with the distributions of the other three configurations as a terminal stage in a sequence of gradual resorption. I therefore tentatively suggested that this configuration represented a resorption process different from the process spreading from the pore canal pores.

Discussion

Discussions of the biology of cosmine usually consider either the significance of cosmine as a functional unit of the body — how different biological processes like deposition, growth and resorption took place, or the significance of the pore canal system. As stated above, it is the latter problem that will be discussed here.

Current views. The current view is that the pore canal cavities were occupied by sensory organs. Denison (1947, p. 350, Text-fig. 7, Pl. 3, fig. 2; 1951, p. 204, Text-fig. 37), Bölau (1951, p. 32, Text-fig. 2) and Gross (1956, p. 56, Text-figs. 35, 37, 40, 42) showed that among some osteostracans and osteolepiforms there was continuity between the pore canal system and the cavities of the sensory canals and pitlines. It was also claimed (Denison, 1947, p. 350, Text-figs. 5, 6; 1951, Text-fig. 32; Bölau, 1951, Text-figs. 3,7) that the configurations of osteostracan pore canals, as seen in transverse section, were similar to those of the lateral lines. Both had dorsal and ventral parts separated by a sieve plate. These authors, therefore, associated the pore canal system with the lateral lines.

Thomson (1977, p. 257) suggested that the pore canal cavities contained electroreceptors. His reasons for this were: (1) The organs in the pore canal cavities were probably not mechanoreceptors, because the lateral line system itself was well developed in these forms (Thomson, 1977, p. 263), and because the dimensions of the pore canal cavities are much smaller than those of the mechanoreceptors. (2) He also claimed similarities in spacing, size and shape between electroreceptors in bony fishes and the pore canal cavities (Thomson, 1977, p. 265). (3) The electroreceptors of modern fishes are often situated in a material of high electrical resistivity, and dentine is such a substance (Thomson, 1977, p. 265). Meinke (1987, p. 140) used as an argument that most primitive fishes seem to have electroreceptors. This interpretation seems to be supported by several authors (e.g. Northcutt and Gans, 1983, p. 16; Meinke, 1984, p. 464; 1987, p. 140; Gans, 1987, p. 373).

Critique of arguments for a sensory function. The continuity between mesh canals and grooves for pitlines and sensory canals is no proof that these canals have the same function (contrary to Pearson, 1984, p. 54). It seems e.g. likely that vessels from a dermal vascular plexus occupying the pore canal system would pass through the cavities for the sensory canals is no proof that these canals had the same function (contrary to Pearson, 1984, p. 54). It seems e.g. likely that vessels from a dermal vascular plexus occupying the pore canal system would pass through the cavities for the sensory canals and pitlines. Gross (1956, p. 38) pointed out that a continuity between pitlines and pore canal system existed only when the former ran in the dentine. This suggests that the continuity is due not to common function, but rather to the position of the pitline within the cosmine.

Meinke (1984, p. 465; 1987, p. 140) pointed out that electroreceptory ampullary organs do not communicate directly with each other. Thus, the system of canals connecting the pore canal cavities is an argument against an electroreceptive function of the pore canal cavities.

Thomson (1977, p. 263) stated that possible sensory organs in the pore canal cavities were different from the lateral line organs. There are, to my knowledge, no examples of such different sensory organs showing such a continuity with each other. Thus, the continuity is unlikely to be an indication of closely related functions.

It is interesting, with regard to the claimed similarity in structure between pore canal and lateral line canals in osteostracans, that some authors (Schultze, 1969, p. 56, Text- fig. 42; Ørvig, 1969, p. 243; cf. also Miles, 1977, p. 312) are sceptical of a homology between the pore canals in osteostracans on the one hand and rhipidists and dipnoans on the other. If these structures are non-homologous, the argument in support of similarity in structure between pore canals and lateral line canals on osteostracans fails. I also believe that a bipartition of lateral line canals by a sieve-plate, like that described for these osteotracans, is comparatively rare among gnathostome fishes (e.g., Harder, 1975, Text-figs. 246-248). Can it be that the bipartiton represents a division into a proximal vascular part and distal sensory part (cf. Gross, 1968, p. 75)?

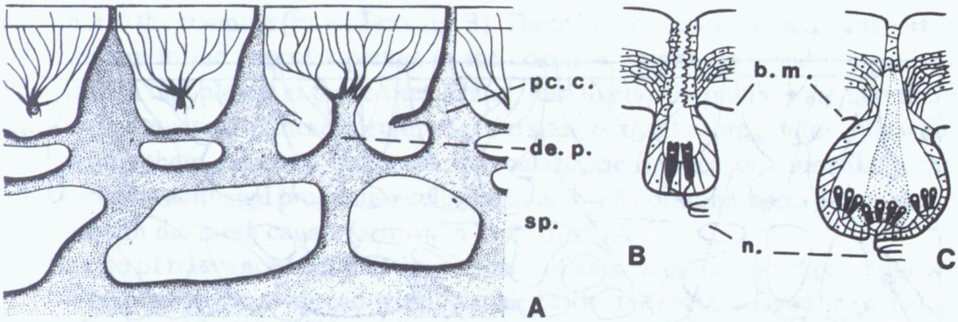
The presence of electroreceptors in several groups of fishes is not a good argument that the pore canal cavities of osteolepiforms are sensory organs. It is possible that the epidermis of e.g. osteolepiforms included such organs, but they need not have had any connection with the pore canal system. Meinke (1984, p. 465) pointed out that it is rare that ampullary organs penetrate into the dermis to any great extent (cf. also Jörgensen, 1980, Text-fig. 1; Jörgensen, 1982, pp. 211, 213, Text-figs. 12H, K, but also Text-fig. 12J; Fritzsch and Bolz, 1986, Text-figs. 3a, c, e, g). Besides, if osteolepiforms had electroreceptors, I find that a structure like the small clusters of pits in the cosmine described in osteolepids by Jarvik (1948, p. 137; 1950, p. 98, grp.so., e.g. Text-figs. 13-16) and Bjerring (1972, p. 85, Text-figs. 1-4, 6), in *Powichthys* by Jessen (1980, grp.so, Text-fig. 3A), and in *Youngolepis* by Chang (1980, p. 23, grp.so, Text-fig. 5B), are more likely to represent remains of electroreceptors. Bjerring (1972, Text-fig. 6B) showed that the nerves from these organs probably ran near the nerves from the lateral line organs.

An argument against the pore canal cavities having contained electroreceptors is their even distribution all over the body. Electroreceptors in extant forms are generally arranged in clusters or concentrated to certain areas (cf. Friedrich-Freksa, 1930, Figs. 2,3; Jörgensen et al., 1972, Fig. 1; Jörgensen, 1980, Fig. 1; Szabo et al., 1972, Fig. 3; Szabo, 1974, Text-figs. 21, 22 for fishes; and Fritzsch and Wahnschaffe, 1983, Text-fig. 19 for amphibians). The distribution of electroreceptors is more reminiscent of that of the above-mentioned clusters of pores.

If the pore canal cavities did not contain sensory organs, what function did they have? My interpretation is that they were mainly vascular. This is supported by the following observations.

The pore canal tubes are the only connections between the interior of the animal and the epidermis. Thus, nourishment to the epidermal cells through the tight cosmine cover, must have been by way of the pore canals. The pore canals, therefore, presumably included, at least partly, blood vessels, either by way of a loop, or a sinusoid.

The canals leading to the pore canal cavities, the mesh canals and the oblique canals, have diameters roughly about half or one third of the diameter of the cavity (Gross, 1956, Pl. 11, fig.1, Pl.11, fig.2, Pl.12, fig.4). This is in contrast to the relative sizes of the opening for the tiny nerve entering the cavity of an electroreceptor (Text-fig. 2) and that of the cavity for this organ, as shown in e.g. gymnotids by Szabo (1965, Text-fig. 1, 2, 10, 11B; 1974, Text-figs. 3, 13) and Harder (1975, Text-fig. 256), for the ampullae of Lorenzini in the siluroid *Plotosus anguillaris* (Friedich-Freksa 1930, Text-fig. 4), and for urodeles (Fritzsch and Wahnschaffe, 1983, Text-fig. 22). This difference indicates that there are vessels entering the

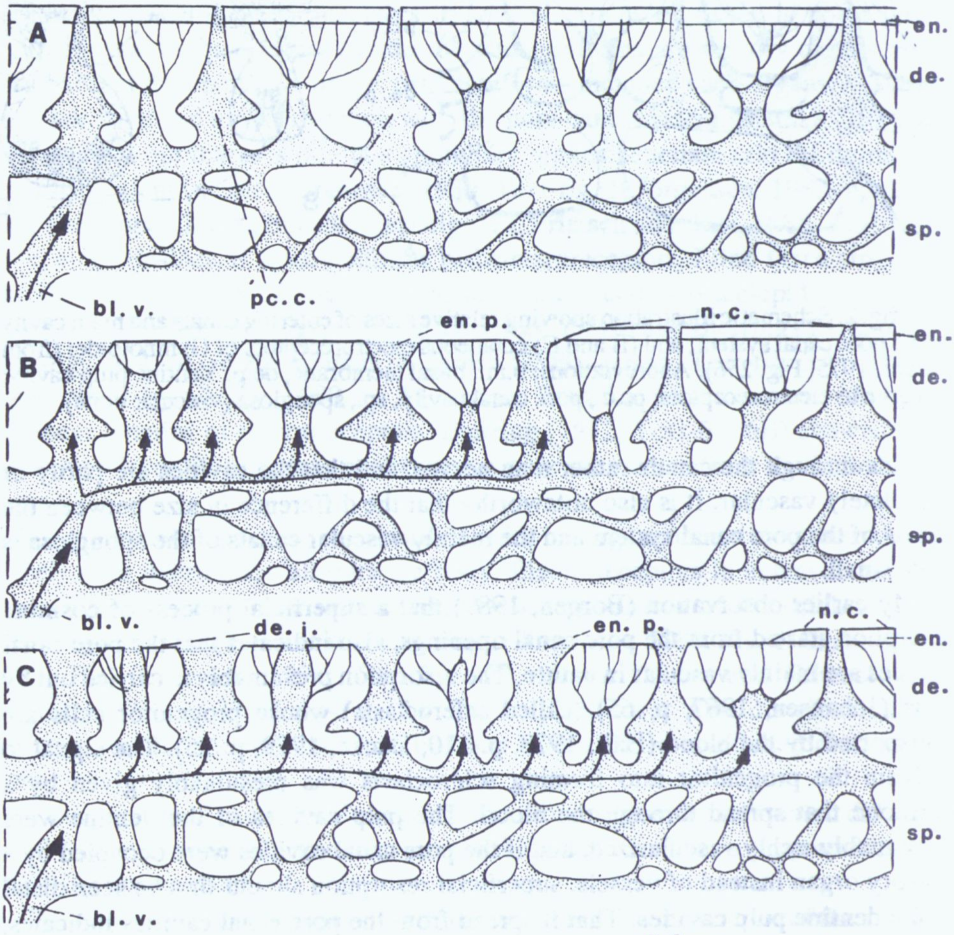


Text-fig. 2. Schematic illustration showing relative sizes of entering canals and main cavity in (A) pore canal system, and (B and C) cutaneous electroreceptors of Gymnotoidei (from Harder, 1975, Fig. 256). Abbreviations; b.m., basal membrane; de.p., dentine pulp cavity; n., nerve to electroreceptors; pc.c., pore canal cavity; sp., spongiosa (vascular bone).

cavities through the canals rather than nerves, and that the cavities are partly or completely vascular. It is also noteworthy that the difference in size between the canals of the pore canal system and the mainly vascular canals of the spongiosa is quite small.

My earlier observation (Borgen, 1989) that a superficial process of cosmine resorption started from the pore canal openings, also indicates that the pore canal cavities are mainly vascular in nature. The resorption presumably is carried out by cells (Johansen, 1967, p. 65) (called scleroclasts) whose progenitor cells are transported by the blood (Hall, 1978, p. 110; Dacke, 1979, p. 25). The signal to activate the progenitor into forming scleroclasts was presumably given by a hormone that spread through the blood. The pulp cavities of the dentine were presumably richly vascularized, and if the pore canal cavities were occupied by a sensory organ instead of vessels, superficial resorption should first be seen distal to the dentine pulp cavities. That it spread from the pore canal cavities indicates, therefore, that this cavity was more vascularized than the pulp cavity.

It may be relevant that the distinct stages of superficial resorption spreading from the pore canal openings, have as yet been observed only on a single specimen. It is not quite clear to me whether Thomson (1977, p. 251, Text-fig. 4) saw these stages on the specimen of *Megalichthys hibberti* he described, but he did not indicate their presence. This apparent rarity can be due to researchers not having looked thoroughly enough for it on their material. The specimen that was mapped (referred by Jarvik, 1948 to *Gyroptychius milleri*) has been known since at least 1948 without these structures being observed. It can also be due to the process being completed very rapidly, and therefore is rarely preserved. A rapid resorption process might need to have a large number of scleroclasts available. If so, a reservoir of scleroclast progenitor cells would be required, and a possible function of the pore canal cavities is as would be such a reservoir.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An observation that also requires explanation is that superficial resorption spread from only a few sites. This might be due to the course of dermal blood vessels proximal to the cosmine (bl.v., Text-fig. 3). These blood vessels, which transported the hormone to the vascular plexus in the cosmine, might have had their initial contact with that plexus at those sites. Other, less likely, alternatives are that there was local production of these hormones at the sites, or that the progenitor cells were present only there. Anyway, either the scleroclasts themselves, or, more likely, the substance that activated progenitor cells, presumably a hormone, spread from those sites through the mesh canals (arrows in Text-figs. 3A-C).

It is also of relevance here that the presence of an area of expanded pores shows that the resorption agent spread within canals below the surface faster than on the surface. If it had not done so, we would have had a single resorption front (Text-fig. 3D), and not the zone of expanded pores that we had observed (en.p., Text-figs. 3B, C). It is possible that the margins of the areas of complete resorption are of this type.

From the above it seems clear that the pore canal cavities might include a vascular part. A natural question is then: (1) Did the pore canal cavities have a function in addition to containing blood vessels? If so, what function was the dominant one? Were the blood vessels just tiny capillaries running in the side walls of e.g. a sensory organ, or was the main cavity filled by a blood vessel, and did small nerves run along the side wall?

Regarding the first question, it is noteworthy that, to my knowledge, no indication of differentiation of the pore canal cavities has been observed. This suggests that the cavity had, or at least was dominated by, one function. I found that the smooth transition from the vascular canals of the spongiosa to the cavities of the pore canal system indicated that the main part of those cavities were vascular. It seems likely that nerves to the epidermis also passed through the pore canal cavities, but these presumably represented a minor part of those cavities.

Concluding comments. I support Thomson's statement (1977, p. 265) that it is not possible to arrive at a definite answer as to how the pore canal system functioned in early fishes. At least not yet. However, the idea that the pore canal system, in e.g. osteolepids primarily had a sensory (possibly electro-sensory) function, which now appears to be accepted by many (e.g. Miles, in Moy-Thomas and Miles, 1971, p. 112; Northcutt and Gans, 1983, p. 16; Meinke, 1984, p. 464; 1987, p. 135; Gans, 1987, p. 373), seems to me unlikely. As I have tried to show,

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Text-fig. 3. Schematic reconstructions of superficial resorption seen in transverse sections. A: Normal cosmine. B: Initial stage of superficial resorption, where a hormone, symbolized by the arrows, has entered the pore canal cavities to the left. C: The influence of the hormone has passed on to the right. Cavities and pores have expanded further, leaving dentine islets. The pores to the right have also been expanded. D: Sketch showing a reconstruction of how a section of the resorption front might look if the resorption had not spread through the vascular system of the cosmine.

Abbreviations: bl.v., blood vessel; de., dentine; de.i., dentine islets; en., enameloid; en.p., enlarged pores; n.c., normal cosmine; pc.c., pore canal cavity; sp., spongiosa (vascular bone).

it seems more probable that the pore canal system, at least in osteolepids and porolepiforms, was primarily a vascular system and that the pore canal cavities might have contained a vascular loop, or a sinusoid. It should be noted that the hypothesis that the pore canal system being a major part of the cosmine, had as its main function to facilitate the resorption of the tissues, which fits into the hypothesis that an important function of the dermal skeleton is as a store for calcium and phosphates (cf. e.g. Halstead, 1974, p. 38; Thomson, 1975, p. 42; Hall, 1978, p. 21; but see also Denison, 1963, p. 150; 1970, p. 13).

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Functional morphology of the feeding mechanism in a primitive palaeoniscoid-grade actinopterygian fish

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Abstract. An elevated coronoid process along the posterior dorsal border of the mandible is an important feature of the feeding mechanism in neopterygian actinopterygians. It serves as an insertion point for a portion of the adductor mandibulae muscle, as well as an attachment surface for a ligament that extends from the maxilla. Together, these act to increase bite strength and jaw stability and allow for more torque about the jaw joint. The presence reported here of a well-developed coronoid process on the mandible of an Upper Carboniferous "palaeoniscoid" indicates that this morphological innovation occurs in a more primitive actinopterygian than has been known previously. It also provides evidence that the coronoid process evolved (at least once) independent of the acquisition of other feeding-related advancements (vertical preoperculum, reduced maxilla, more kinetic skull, larger adductor muscle) with which it was thought to have coevolved. The early evolutionary history of the actinopterygian feeding mechanism was therefore likely more complicated than the "major adaptive levels" model that has been advocated.

Introduction

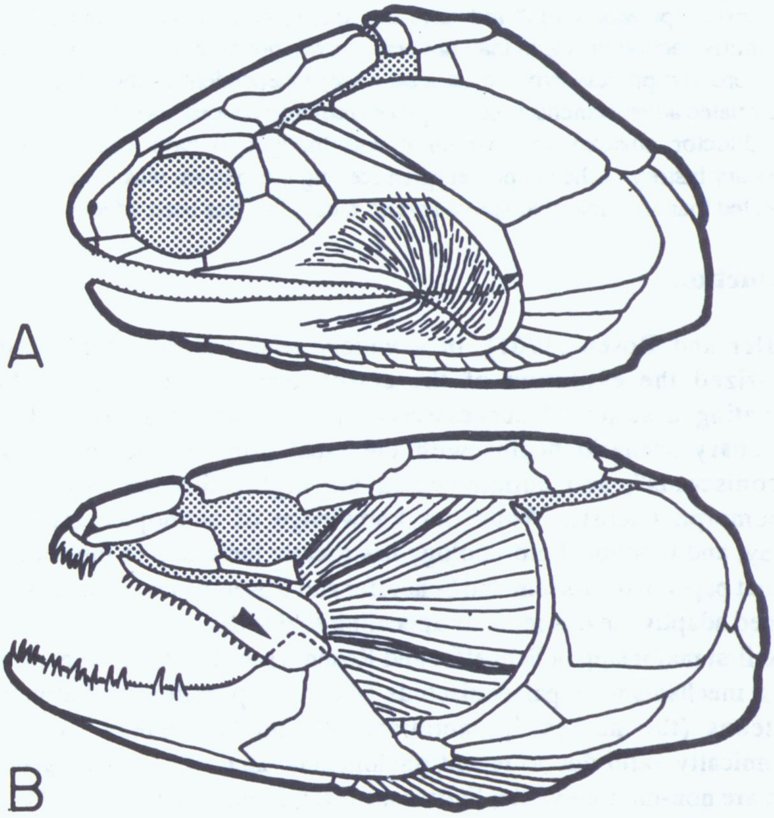
Schaeffer and Rosen (1961), in a widely read and commonly cited paper, summarized the evolution of the actinopterygian feeding mechanism as representing a series of successively more advanced adaptive levels. This evolutionary scenario begins with the most primitive actinopterygians, the "palaeoniscoids", and culminates in the highly derived protrusible-jawed acanthomorph teleosts. While our knowledge of actinopterygian phylogeny, anatomy, and functional morphology has greatly increased in the nearly 30 years since that paper, it does seem that Schaeffer and Rosen's view of successively more advanced adaptive levels remains appealing to this day.

The first major step in Schaeffer and Rosen's scenario is the transition from the feeding mechanism of palaeoniscoids (the most primitive actinopterygians) to holosteans (the names "palaeoniscoid" and "holostean" are no longer taxonomically valid due to recent phylogenetic analyses indicating that the two groups are non-monophyletic; Patterson, 1982; Lauder and Liem, 1983; Gardiner, 1984). The Actinopterygii as a whole is a well- corroborated monophyletic unit (Patterson, 1982; Lauder and Liem, 1983; Gardiner, 1984).

In primitive palaeoniscoid-grade actinopterygians, such as the Devonian genus *Cheirolepis* (Pearson and Westoll, 1979) and the Triassic form *Pteroniscculus* (Text-fig. 1A), the cheek region is rigidly constructed, and the preoperculum and hyomandibular are oriented obliquely (rather than vertically). The volume of the jaw adductor musculature is relatively small as it is restricted to a palatoquadrate-maxillary adductor chamber that is closed off dorsally by a medial lamina of bone from the preoperculum.

This lamina prevents the adductor musculature from extending upward to the lateral surface of the braincase. The postorbital portion of the maxilla is greatly expanded, and in tight articulation with the surrounding cheek elements. The dorsal margin of the mandible is nearly horizontal and lacks a distinct coronoid process. Overall, the skull is relatively akinetic in contrast with that of more advanced actinopterygians.

At the next (neopterygian) level, typified primitively by the extant halecomorph *Amia* (Text-fig. 1B), the cheek region is more open and the skull as a whole is more kinetic. The preoperculum and hyomandibular are vertically oriented. The relative



Text-fig. 1. Lateral views of actinopterygian skulls. A, a typical "palaeoniscoid" (*Pteroniscultus*) - note rigidly constructed cheek region and relatively small adductor muscle mass (shown as if viewed through the maxilla and mandible). B, a lower neopterygian (*Amia*) - note relatively open cheek region, coronoid process (arrow), and relatively large adductor muscle mass (shown with the postorbital bones removed) reaching the lateral edge of the skull roof. Modified after Schaeffer and Rosen, 1961. Drawn not to scale.

volume of the adductor musculature (no longer confined by an obliquely angled preoperculum with a medial lamina) is greater, with its origin extending to the postorbital portion of the braincase. The maxilla is reduced in size, and lacks a prominent postorbital expansion and extensive articulations with adjacent cheek bones. The mandible bears a distinct, elevated coronoid process along its posterior dorsal border.

The coronoid process is of particular significance. It serves as a insertion point for fibers of the lateral and posterior divisions of the adductor musculature, which in *Amia* (Text- fig. 1B) attach along the posterior edge and posteromedial surface of the process. The remainder of the adductor muscle mass inserts into the Meckelian fossa of the mandible. In addition, a maxillomandibular ligament extends from the posteromedial portion of the maxilla to the lateral surface of the coronoid process. This ligament, and the pattern of muscle insertion into the coronoid process, act to increase the amount of torque that can be developed about the jaw articulation and thereby increase bite strength, as well as provide for greater stability of movement during feeding. In Schaeffer and Rosen's view the presence of a coronoid process has the effect of transforming the posterior of the mandible from a straight to a more mechanically efficient bent level arm. Schaeffer and Rosen (1961, p.191) summarized the importance of the coronoid process as follows: "... the palaeoniscoid adductor was less powerful and the torque about the jaw articulation far below that in forms with a coronoid process on the mandible."

A coronoid process is commonly developed in neopterygian actinopterygians (Ginglymodi plus Halecomorphi plus Teleostei). Gardiner (1984) considered the presence of the process to be a neopterygian synapomorphy. The intent of this paper is first, to document the presence of a well-developed coronoid process in a primitive fossil "palaeoniscoid," and second, to consider what implications the presence of this process has relative to previous interpretations concerning the early evolution of the actinopterygian feeding mechanism.

Materials and methods

A total of 36 palaeoniscoid mandibles from two Upper Carboniferous (Carbondale Formation; Westphalian lower D) localities in western Indiana, USA, were examined for this study. The specimens were collected at the Bethel and Logan black shale quarries; the location, palaeoecology and biota of these sites were discussed in detail by Zangerl and Richardson (1963).

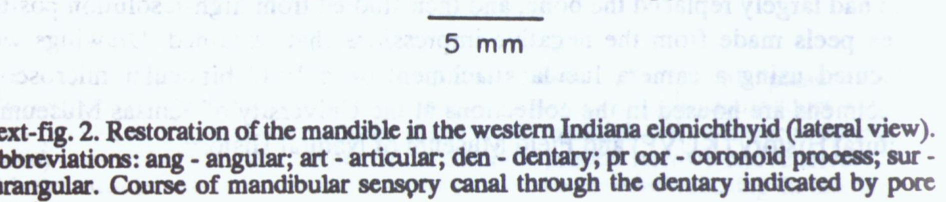
In most cases, specimens were prepared using a fine needle to remove pyrite that had largely replaced the bone, and then studied from high-resolution positive latex peels made from the negative impressions that remained. Drawings were executed using a camera lucida attachment on a Wild binocular microscope. Specimens are housed in the collections at the University of Kansas Museum of Natural History (KUVP) and Field Museum of Natural History.

The material discussed here is interpreted as occupying the number of Carboniferous genera, including *Elonichthys*, *Rhadinichthys*, and *Kansasiella*. The precise interrelationships of fishes at this level remain unclear (see Gardiner, 1984, for a discussion of these forms). The material appears to be closest to *Elonichthys* on the basis of its general proportions, dermal ornamentation, and scale morphology (following the diagnosis in Gardiner, 1963). It is therefore referred to in this paper as "elonichthyid", with the understanding that Schultze and Bardack (1987) considered the genus *Elonichthys* itself to be non-monophyletic. Elonichthyids are relatively common in contemporaneous faunas, notably Mazon Creek (Schultze and Bardack, 1987, and references therein). They are more advanced than the most primitive fossil actinopterygians (the Devonian genera *Cheirolepis*, *Mimia* and *Moythomasia*) but less derived than fossil genera such as *Platysomus*, *Boreosomus* and *Perleidus* which are phylogenetically close to extant neopterygians (Gardiner, 1984).

Description

The mandibles examined (which include both isolated elements and mandibles associated with partial skeletons) have a well- developed coronoid process (Plate). The process is present as a distinct, approximately symmetrical rounded projection extending above the dorsolateral margin of the mandible; it is just anterior to the articular bone, which bears the cotyle for articulation with the quadratojugal.

Although the coronoid process is partially broken in some specimens, its size and shape can be readily interpreted in most cases from impressions left in the shale. It appears to be formed entirely by a relatively thin lamina of bone extending dorsally from the main part of the surangular (Text-fig. 2), and is located immediately above a smooth, semicircular depression in that element. This depression, which is devoid of ornamentation, is the area where the posteroventral corner of the maxilla overlaps the end of the mandible.



Text-fig. 2. Restoration of the mandible in the western Indiana elonichthyid (lateral view). Abbreviations: ang - angular; art - articular; den - dentary; pr cor - coronoid process; sur - surangular. Course of mandibular sensory canal through the dentary indicated by pore openings.

The coronoid process generally bears a few relatively prominent teeth along its anterior edge. Owing to the curvature of this leading edge, these point more anteriorly than dorsally (Text- fig. 2), and in some specimens extend out at nearly 90 degrees to the orientation of the dentition along the the dentary.

Discussion

The presence of a coronoid process in a relatively primitive elonichthyid "palaeoniscoid" has some implications for our understanding of the early evolution of the actinopterygian feeding mechanism. Gardiner (1984) listed the presence of an almost vertical preoperculum and hyomandibular, and a maxilla and preoperculum detached from the palatoquadrate, as synapomorphies uniting *Platysomus, Boreosomus, Perleidus* and neopterygians. These features have strong functional correlates and figure prominently in the structural transition from the primitive feeding mechanism of palaeoniscoid-grade actinopterygians to the more advanced mechanism of neopterygians and their immediate fossil relatives. Schaeffer and Rosen (1961), as well as Gardiner (1967) and Moy-Thomas and Miles (1971), considered the presence of a well-developed coronoid process, along with a vertically oriented preoperculum, larger adductor muscle, and more open cheek region, to be structural innovations that appear at the neopterygian level.

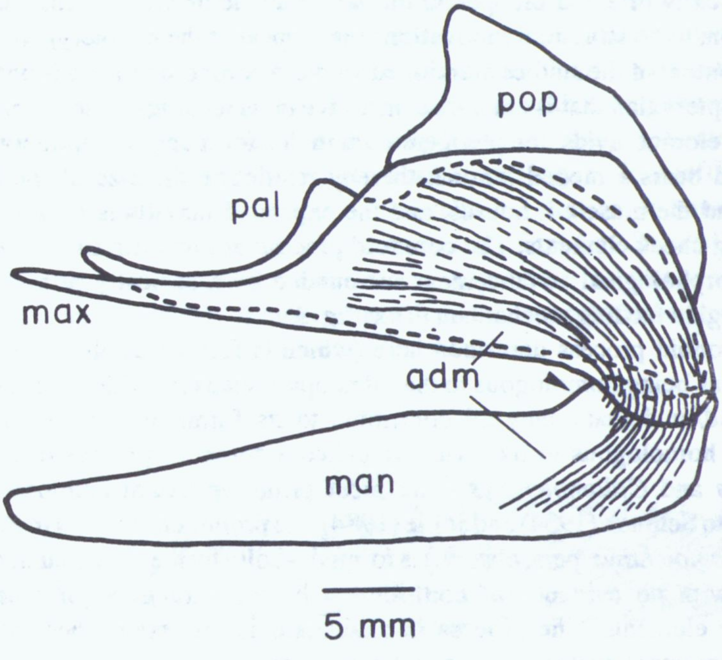
In the context of the studies mentioned above, a coronoid process is out of place in an actinopterygian that is otherwise primitive in its feeding-related morphology. As in other elonichthyids, the preoperculum in this form angles obliquely over the maxilla and bears a medial lamina, thereby restricting the size of the adductor chamber and the muscle it houses, and the expanded maxilla is firmly joined to surrounding cheek elements. The coronoid process of this form can be seen as an isolated morphological advancement surrounded by a basically primitive lower actinopterygian feeding mechanism (Text-fig. 3).

The coronoid process described here (which is formed by the surangular) is interpreted as being homologous to that of neopterygians (in which the surangular, angular, and/or dentary may all contribute to its formation). It should not be considered homologous to the structure called a coronoid process in cladistians (*Polypterus* and *Calamoichthys* - the most primitive extant actinopterygians). According to Schmäh (1934) and Jollie (1984), the prominent process in *Polypterus* (and in *Calamoichthys*, pers. observ.) is formed wholly by the prearticular (a medial element), with no evidence of contribution by the surangular or other lateral mandibular elements. The process in cladistians is interpreted here as being a probable functional analogue, but non-homologous.

Other relatively primitive fossil actinopterygians are known to possess a somewhat weakly developed coronoid process. However, these taxa (including aeduellids and "subholosteans"; Gardiner, 1967) are more phylogenetically derived than elonichthyids, and also have other functionally important features such as a reduced maxilla and more vertically aligned preoperculum. They are therefore closer to approaching a neopterygian-level feeding mechanism.

It is possible to speculate as to how the coronoid process described here would have improved feeding efficiency.

Presumably, as in other fishes, a portion of the adductor muscle inserted on the coronoid process and thereby increased torque about the jaw articulation (Text-fig. 3). In addition to acting as an insertion point for the adductor musculature, the process could also have been an attachment point for a maxillomandibular ligament extending from the medial surface of the posteroventral flange of the maxilla to the lateral surface of the coronoid process. Maxillae from the western Indiana elonichthyid have a raised bump on their medial surface which is positioned so that it would be opposite the coronoid process when the maxilla and mandible are in their natural positions. A ligament extending between the coronoid process and the maxilla would enhance performance by providing for greater stability of maxillary movement during feeding (Lauder, 1979).



Text-fig. 3. Composite semi-diagrammatic reconstruction of elements involved in the feeding mechanism of the western Indiana elonichthyid. Abbreviations: adm - adductor mandibulae muscle; man - mandible; max - maxilla; pal - palatoquadrate; pop - preoperculum. Coronoid process indicated by arrow; palatoquadrate shown by dashed line where overlain by maxilla.

The net increase in feeding performance in the elonichthyid discussed here was probably relatively small because the other morphological specializations with which a coronoid process is typically associated only occur in more functionally and phylogenetically derived fishes. The occurrence of a coronoid process in the western Indiana elonichthyid does indicate that the feature evolved (at least once) independent of its appearance with other feeding-related morphological advancements is generally taken as characterizing the structural transition from "palaeoniscoids" to lower neopterygians. Its presence also provides evidence that the early evolution of the actinopterygian feeding mechanism was more complex than the relatively simple major adaptive levels model of Schaeffer and Rosen (1961).

Adopting the terminology of Lauder (1982), the coronoid process, at its earliest known appearance, is not functionally coupled with the other feeding-related innovations that first evolved in early neopterygians. It therefore should not be treated (as in the past) as a structural component in a predictable historical pattern of change in the evolution of the actinopterygian feeding mechanism.

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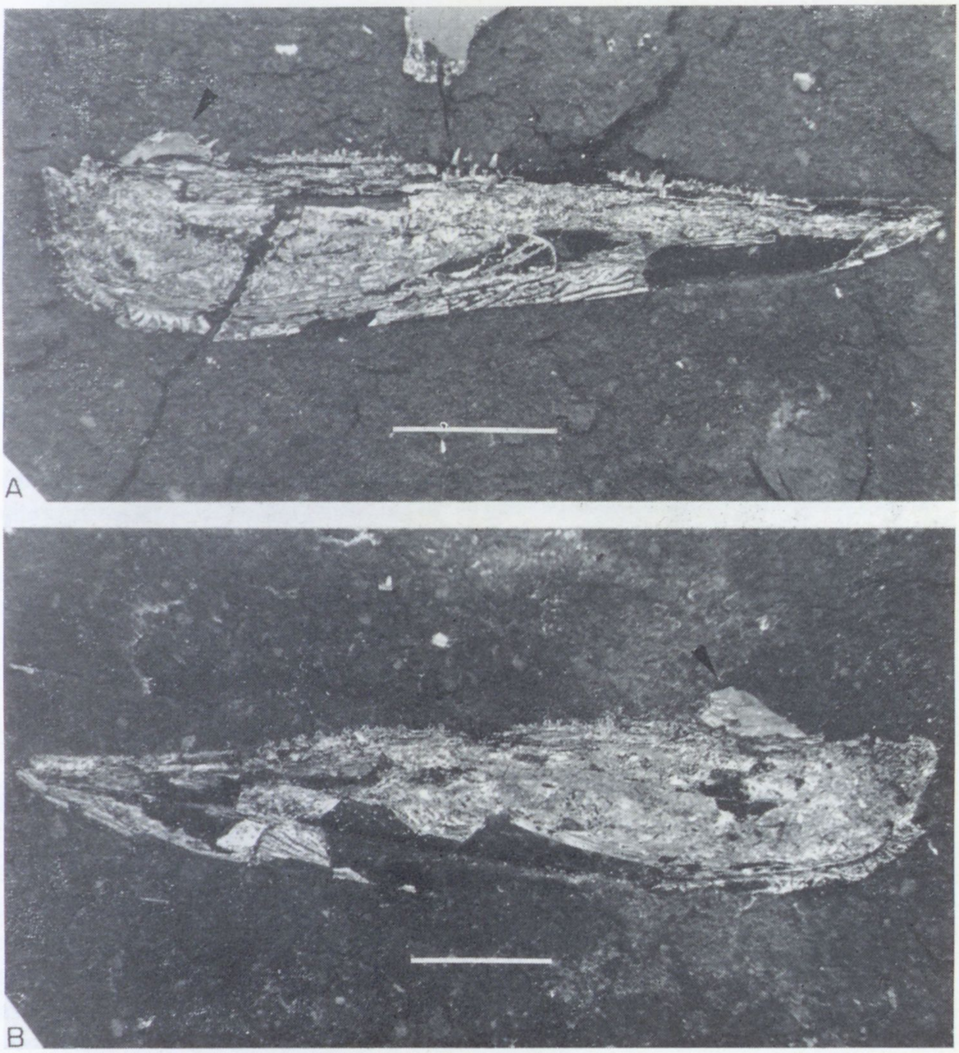
Plate.

Elonichthyid-level mandibles with a coronoid process (indicated by arrows) from the Uppe Carboniferous (Carbondale Formation: Westphalian lower D) of western Indiana, USA. A, KUVP 101702. B, KUVP 80300. Photographed under alcohol. Scale bars = 5 mm.


A
B

Some aspects of biomineralization of vertebrate exoskeleton

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Abstract. Agnathan and arthrodire exoskeletal plates have been studied together with the plates of turtle carapace at different stages of ontogeny. In bones bioapatite crystals occur inside the collagen fibril, their prismatic facets being oriented parallel to the longitudinal axis of the fibril. At the turtle's hatching stage, both sides of the plates show the presence of crystallic matter. The amount of bioapatite increases during the turtle's growth, being more intensive at the basal side until it reaches the age of three and becoming equal on both sides afterwards. During the period of up to 3 years, the basal layer of the plate is formed ; its external side, however, bears numerous vertical bony trabeculae. Collagen fibrils and apatite crystals are oriented perpendicular to the plate surface. In this way the spongy layer is formed. By the 4th year of life, three plate layers become completed.

During the fossilization of the bony plates crystals grow in size without loosing their orientation. In juvenile arthrodire specimens in the outer layer the orientation of crystals is similar to that in young turtles. In adult arthrodires the layers become equal. The similarity in the plate structures might be explained by the general rules of exoskeleton formation — by the appearance of different plate layers at different times, and also by the general processes of vertical growth of dermal ossification during ontogeny.

The purpose of this study was to investigate the mineral exoskeleton composition of some Devonian vertebrates. The authors studied the plates of the agnathan (Psammosteidae) and the arthrodires (*Plourdosteus*). Besides, the plates of trunk armour of 2 turtle species — *Testudo graeca* and *T. horsfieldi* — showing different stages of ontogenetic development were investigated to study the process of biomineralization of the living exoskeleton. It would allow us to gain a better understanding of the characteristic features of bone biomineralization of fossil vertebrates.

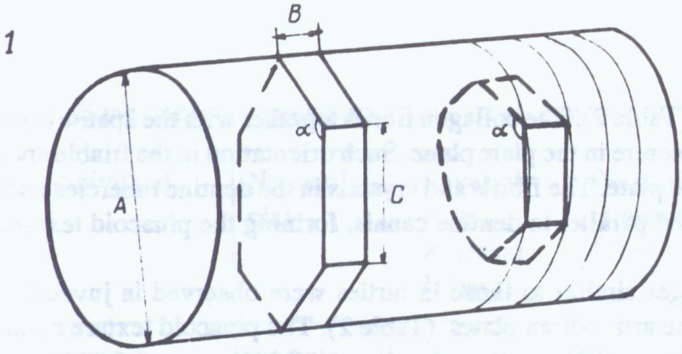
In this case histological and mineralogical methods were used with the main emphasis on the X-ray diffraction method, which enabled to reveal the orientation of the internal mineral-organic component of a bone.

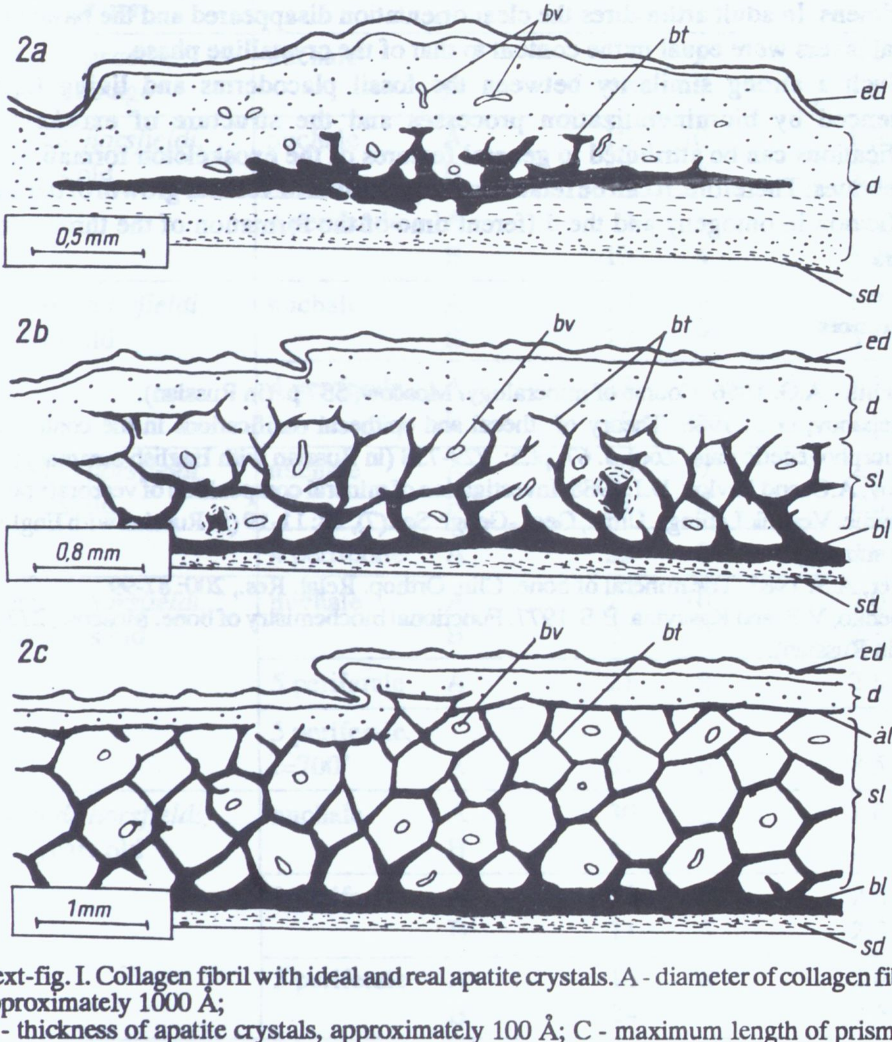
The hard bone tissue is a mixture of calcium phosphate and collagen fibrils (Torbenko and Kasavina, 1977). The bone mineral in living vertebrates is amorphous calcium phosphate and crystalline hydroxy-carbon-apatite (dahllite) (Posner, 1985). Non-biogenetic apatite crystals are elongate, prismatic to tabular in shape (Betekhtin, 1956). The bone apatite of the studied vertebrates is represented by tabular forms. The crystals have pinacoid and prismatic facets. Hexagonal tabular crystals occur inside the collagen fibril, and so pinacoid facets are normal to the longitudinal axis of the collagen fibril (Text-fig. 1). The ideal crystals are equal in size to the fibril diameter. The real apatite crystals are smaller and their angles are sometimes not hexagonal. Using X-ray diffraction, such an orientation of the crystals may help to define the direction of fibril. Among the reflections from atomic lattices, the prismatic and pinacoid reflections {300}, {002} and reflection {211} are well expressed on the diffractograms. Some others are quite weak (Ivanov and Pavlov, 1988). The orientation of apatite crystal and collagen fibril of the upper layers of vertebrate plates can be estimated from the prismatic to pinacoid intensity reflection ratio: if this ratio is less than 2, the pinacoid facets of the crystals are oriented parallel to the plate surface (i.e. pinacoid texture); if the ratio is more than 4, the prismatic facets of crystals are parallel to the surface of the plate (i.e. prismatic texture); by ratios from 2 to 4, the crystals exhibit different orientations.

. Table 1 shows the results obtained in the study of turtle plate biomineralization. In turtle embryos with carapace length of 20 mm the nuchal plate is a perforated bony plate. It consists of many tangling trabecula (Cherepanov, 1988). The bone layers are not clearly expressed (Text-fig. 2,a); however, the crystalline apatite was found on the basal side of the plate. After hatching, apatite crystals occur on the external (apical) and basal layers of the nuchal plate. The crystalline phase increases with age. Starting from the 3rd year, the apatite is rather more accumulated on the basal side than on the external side. The turtle of this age shows pinacoid texture on the external side of the nuchal and peripheral plates, i.e. the collagen fibrils are normal to the plate surface. Such an orientation may be ascribed to the intensive growth ossifications in the upper dermal layers marked by the presence of numerous vertical bony trabecula (Text- fig. 2,b). It is such a way that the spongy layer of plates was formed. At this stage the thin basal layer is formed, in fact, such ossification in the dermis does not increase and the apatite crystals and collagen fibrils in the basal layer show different orientation (with the ratio of reflection intensity from 3 to 4). At the age of 3 the apical layer has not been formed as yet.

In a 4-years-old turtle the formation of the histological structure of the dermal ossification is terminated. Three layers: external (apical) and basal layers of compact bone tissue and internal, spongy layer are easily discernible in the plate (Text- fig. 2,c). The soft derma strongly decreases, and the bone plate occupies the entire area from epidermis to subdermis. The external and basal layers are approximately equal in the content of the crystalline phase. The texture disappears, the apatite crystals and collagen fibrils show different orientation.

The bone mineral of the Devonian vertebrates can be placed somewhere between the phosphate of living vertebrates and non- biogenetic apatite (francolite)(Ivanov and Pavlov, 1988). In the process of the fossilization of the bone tissue the bioapatite crystals increase, yet the texture does not change. Therefore, we can restore the living orientation of collagen fibrils in fossil bone and compare it with the living bone tissue. The prismatic texture ·is to be found on the basal layers of the





Text-fig. I. Collagen fibril with ideal and real apatite crystals. A - diameter of collagen fibril, approximately 1000 Å;

B - thickness of apatite crystals, approximately 100 Å; C - maximum length of prismatic facet: α - hexagonal angle (120°) of pinacoid facet.

Text-fig. 2. Schematic representation of the histological sections through skin in nuchal plate region of the carapace in the turtle *Testudo graeca*: a) embryo with carapace length 20 mm; b) I year old juvenile; c) 4 years old juvenile. al - apical layer of bone, bl - basal layer of bone, bt - bony trabeculae, bv - blood vessel, d - dermis, ed - epidermis, sd - subdermis, sl - spongy layer of bone.

psammosteid plates (Table 2). The collagen fibrils together with the apatite crystals form the compact structure in the plate plane. Such orientation in the friable spongy layer consolidated the plate. The fibrils and crystals in the dentine tubercles and the tesserae were disposed parallel to dentine canals, forming the pinacoid texture on the surface.

Development stages similar to those in turtles were observed in juvenile and adult specimens of the arthrodiran plates (Table 2). The pinacoid texture could be traced in the external layer of juvenile arthrodires, and it disappeared with age.

The crystals and fibrils were better oriented in the basal layer of the young specimens. In adult arthrodires the clear orientation disappeared and the basal and apical layers were equal in the content to that of the crystalline phase.

Such a strong similarity between the fossil placoderms and living turtle evidenced by biomineralization processes and the structure of exoskeletal ossifications can be attributed to general features of the exoskeleton formation in vertebrates. Therefore, it can be related to the processes of vertical growth of dermal ossificaton in ontogeny and the different time of the formation of the three bony layers.

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Table 1. Bone mineral characters of turtle trunk armour

Age of individual	Name of plate	Layer of plate: A-apical B-basal	Reflection intensity		Ratio of reflection {300} to {002}
			{300}	{002}	
Testudo graeca, embryo with carapace length 20 mm	nuchale	A	0	-	-
		B	2	-	-
Testudo graeca, hatching stage	nuchale	A	7	5	1.4
		B	12	4	3.0
Testudo horsfieldi, 2 years old	nuchale	A	10	10	1.0
		B	15	4	3.8
	4 periferale	A	7	5	1.4
		B	13	4	3.2
Testudo horsfieldi, 3 years old	nuchale	A	15	9	1.7
		B	27	8	3.4
	4 periferale	A	13	6	2.2
		B	10	4	2.5
Testudo horsfieldi, 4 years old	nuchale	A	20	9	2.2
		B	21	8	2.6
	4 periferale	A	22	8	2.8
Testudo horsfieldi, 5–6 years old	nuchale	A	20	10	2.0
		B	21	9	2.3
	5 periferale	A	21	8	2.6
	5 periferale, t=700°	A	51	6	8.5
Testudo horsfieldi, 6-7 years old	nuchale	A	30	15	2.0
		B	27	12	2.3
	1 periferale	A	12	6	2.0
		B	11	5	2.2
	5 periferale	A	16	8	2.0
		B	24	9	2.6
Testudo horsfieldi, 15 years old	nuchale	A	45	20	2.3
		B	43	15	2.9
Testudo sp.. adult (Paleogene)	nuchale	A	54	23	2.3
		B	41	9	4.5

Table 2. Bone mineral characters of Late Devonian (Early Frasnian) vertebrates.

	Name of plate	Layer of plate: A-external B-basal	Ratio of reflection intensity {300} to {002}
Plourdosteus trautscholdi, Dubnik Formation	$\mathrm{PNu}_{\mathrm{juv}}$	A	1.4
		B	7.6
	$\mathrm{PNu}_{\mathrm{ad}}$	A	2.8
		B	2.4
	$\mathrm{AL}_{\mathrm{juv}}$	A	1.6
		B	4.3
	$\mathrm{AL}_{\mathrm{ad}}$	A	2.1
		B	2.3
	$\mathrm{ADL}_{\mathrm{ad}}$	A	2.5
		B	3.0
Plourdosteus mironovi, Pskov Formation	$\mathrm{AL}_{\mathrm{ad}}$	A	2.0
		B	2.8
Psammosteus megalopteryx, Dubnik Formation	Dorsal plate with tesserae	A	1.8
		B	10.1
	Dorsal plate without tesserae	A	5.2
		B	13.0
	Branchial plate with dentine tubercles	A	1.1
		B	0.9

Tentative synthesis of the heterostracans, Ordovician to Devonian jawless vertebrate, with more general comments on the origin of chordates

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Following recent studies on heterostracan phylogenetic relationships, in connection with D.K. Elliott (Flagstaff), P.-Y. Gagnier (Montreal) and P. Janvier (Paris), I propose here to widen the definition of Heterostraci on the basis of their histology. The Ordovician genera *Arandaspis*, *Sacabambaspis*, *Astraspis* retain primitive features such as several external branchial openings, superficial sensory grooves, pineal-parapineal "opening". Heterostraci sensu stricto or Euheterostraci (Heterostraci Lankester, 1868-70; "crown Heterostraci" Janvier, 1981) are thus characterized by : 1) fused branchiocornual, lateral areas with only one paired, external branchial opening, 2) deep sensory canals, and 3) dorsal and ventral, median growing plates.

Heterostracans are then placed among chordates. They are considered as intermediate between thelodonts and cellular- bonebearing vertebrates (galeaspids and others). Recent discoveries of Cambrian-Ordovician phosphatic microremains, sometimes interpreted as "vertebrate-relatives"' have been re- interpreted as urochordate fossil records. *Pikaia*, from the Middle Cambrian of British Columbia, may be interpreted as a cephalochordate. All these data lead to a more general phylogenetic hypothesis of chordates, with minimum ages for the origin of their main higher taxa.

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Young Upper Devonian antiarch (*Asterolepis*) individuals from the Lode quarry, Latvia

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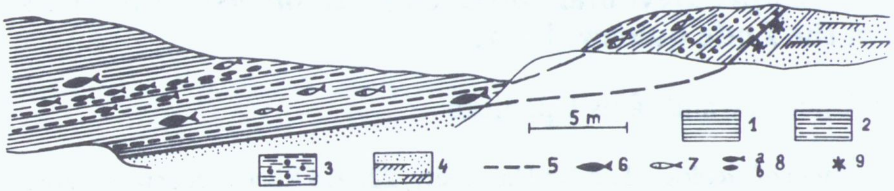
Abstract. Upper Devonian clays of the Lode quarry, Latvia, have yielded numerous well-preserved juveniles of the antiarch *Asterolepis* representing different growth stages. They differ from adult *Asterolepis ornata* in the morphology of the caudal part, body proportions and the ornament of the armour. The visceral skeleton, bones situated in the orbital fenestra and squamation are well preserved.

The taphocoenosis of the Devonian fishes of the Lode clay quarry is characterized by numerous well preserved individuals of one antiarch species - *Asterolepis ornata* (Eichw.), and two species of crossopterygians —*Laccognathus panderi* Gross and *Panderichthys rhombolepis* (Gross) (Lyarskaya and Mark- Kurik, 1972; Lyarskaya, 1981). In this locality remains of psammosteids, acanthodians and conchostracans have also been found. Well-preserved plant macrofossils (*Archaeopteris*) are rather frequent.

The Lode Formation has a rather characteristic lithological composition. There occur dispersed clays unusual in the Old Red facies, containing numerous remains of fishes and other organisms. Red siltstones and sandstones with rare organic remains are common (Kuršs and Lyarskaya, 1973).

In 1989 and 1990 in one of grey dispersed clay lenses (Text-fig. 1) the authors found many complete specimens of previously unknown young antiarchs (see Pl. 1-4). Together with these young fishes there were discovered a few articulated juveniles of acanthodians and crossopterygians which have not been studied yet. Fragments of osteolepidids and adult *Asterolepis ornata* have also been recorded. Rich accumulations of Eumalacostraca (Mysidacea) could be observed in three layers. Entomostraca included some species of conchostracans and several ostracodes (preserved as moulds). The rocks have also yielded fragments of merostomes and many plant remains (*Archaeopteris fissilis* Schmal., *Svalbardia polymorpha* Hoeg and *Platyphyllum* sp. identified by N. Petrosjan, St. Petersburg).

In the bone-bearing lens the organic remains are sorted to a certain degree depending on their shape, size and weight. Near the edge of the clay-filled depression and in the upper part of the bone-bearing layer adult specimens of *Asterolepis ornata* and a larger juvenile of this (?) species were found. Their skeletons were poorly preserved and almost completely leached. Young antiarch individuals occurred in one approximately 1 m thick bed being concentrated within it in a 0.2 m thick layer. Towards the SW edge of the depression in the bone-bearing layer, alongside with complete young individuals, incomplete skeletons of juveniles and their separate armour plates appeared; nearer to the edge the remains of young



Text-fig. 1. Lode quarry section and the distribution of organic remains (by V. Kuršs, unpublished): 1 - clays (mostly greenish-grey), with rare fish fragments and plant macrofossils; 2 - silty clays (mostly multicoloured); 3 - multicoloured gravelstone-clayey pebbles with clayey-silt cement; 4 - massive and cross-bedded fine-grained sandstones; 5 - layers with numerous finds of Mysidacea; 6 - complete specimens of *Asterolepis ornata*; 7 - separafe fish bones (usually 2-5 cm in diameter); 8 - juveniles and small fishes: a - complete specimens, b - separate armour plates; 9 - sulfite nodules.

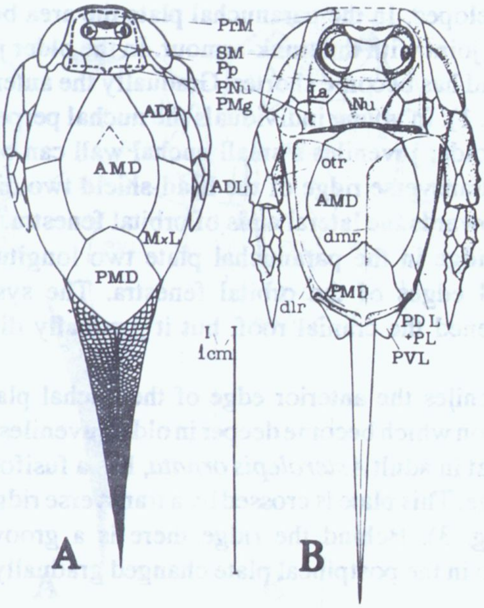
individuals were missing. The juveniles are well preserved, but their skeletons are, as a rule, deformed. The scales covering the caudal part, as well as the orbital bones in the orbital fenestra, are often preserved. Altogether 23 complete specimens, 158 incomplete ones and 55 armour plates have been found in an area of 24 m^2. The length of the head- and trunk-armours of young antiarch individuals is 1.1 - 1.8 cm, comprising about 1/2 of the whole body length. Two incomplete juveniles at later stages of development with the possible body lengths of 2.6 cm (Pl. II fig. 1) and 3.8 cm, respectively, have also been discovered. As the clay layers have been ripped up along the bedding plane, fish skeletons are split into a part and a counterpart (Pl. I fig. 1; Pl. II fig. 5). The specimens are housed in Latvian Nature Museum, Riga, collection no 260.

According to several features the juveniles under consideration belong precisely to the genus *Asterolepis* (see Text-fig. 2). The nuchal plate does not reach the orbital fenestra; the AMD is in contact with the MxL along its posterolateral edge; the semilunar plates (Sm) are paired; the pectoral fins consist of the distal and the proximal segments. Still, the proportions of separate parts of the body differ in young and adult *Asterolepis* specimens (Table 1).

Table 1. Length ratios of body parts.

	head	orbital fenestra	caudal part	proximal segment
	body	head	complete fish	distal segment
Juveniles of *Asterolepis*	0.33-0.42 (n=3)	0.33-0.35 (n=3)	0.90-0.93 (n=2)	0.57-0.88 (n=8)
Adults of *Astrolepis ornata*	0.15-0.21	0.21-0.23	0.33*	up to 1.2-1.3*

n - number of measurements; * after Lyarskaya, 1981



Text-fig. 2. A - reconstruction of adult *Asterolepis ornata*, dorsal view (after Lyarskaya, 1981); B - reconstruction of young *Asterolepis*, dorsal view, chiefly after 260/87 a, b (sensory lines not indicated). PrM - praemedial, La - lateral, Nu - nuchal, Pp - postpineal, PNu - paranuchal, Pmg - postmarginal, SM - submarginal, AMD - anterior median dorsal, PMD - posterior median dorsal, ADL - anterior dorsolateral, PDL - posterior dorsolateral, PL - posterior lateral, MxL - mixilateral plates; dmr -dorsal median ridge of trunk-armour, otr - oblique transverse ridge of AMD, dlr - dorsolateral ridge of trunk armour.

The **head-shield** is known by three specimens belonging to different age groups, and by several fragments. The shield is convex and trapezoidal. Its width is slightly greater than its length. The anterior edge of the head-shield is twice as narrow as the posterior one (in adult *Asterolepis ornata* about 3 times). The lateral edges are straight. The sutures of the bones of the head-shield bear flat and sharp denticles (Pl. III fig. 3).

The anterior part of the cranial roof is bent down. The praemedial plate is very short. The lateral plate is narrow at the orbital fenestra level (Pl. I fig. 3; Pl. III fig. 3). The lateral edge of the lateral plate overlies the submarginal. The submarginal plate is comparatively large and convex. From the contact line with the lateral plate a small ridge proceeds diagonally backwards. In the older juveniles the surface underlying, the lateral plate has an ornament of small longitudinal bands and is separated from the main part of the plate by a low ridge (Pl. II fig. 1a). In the anterior part of this surface there is a flat protruding denticle. Posterolateral corners of the cranial roof have been preserved only in the oldest juveniles. The depression between the paranuchal and postmarginal plates is not developed.

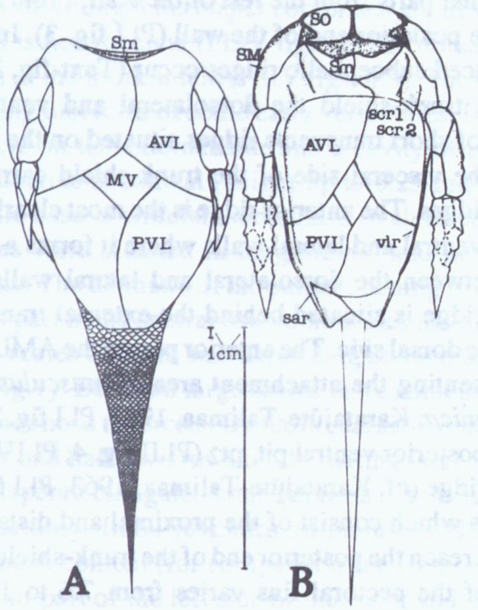
In the nuchal plate there are two depressions separated by a wide medial vault (Pl. III fig. 3). The plate bears a transverse ridge behind which a posteriorly gently sloping area is developed. In the paranuchal plate the area becomes narrower and disappears near the joint with the trunk-armour. In the older juveniles this area has lost its ornament and has become shorter. Gradually the anterior edge of the AMD overlay it (Pl. II fig. 1). In young individuals the nuchal perpendicular wall had not formed yet. In the older juveniles a small nuchal wall can be observed. From the central part of the transverse ridge of the head-shield two diagonal ridges branch out on both sides towards the lateral ends of orbital fenestra. From the lateral ends of the transverse ridge in the paranuchal plate two longitudinal ridges proceed towards the lateral edges of the orbital fenestra. The system of ridges, most probably, strengthened the cranial roof, but it gradually disappeared during the ontogeny.

In younger juveniles the anterior edge of the nuchal plate bore very shallow postpineal depression which become deeper in older juveniles. The postpineal plate, differently from that in adult *Asterolepis ornata*, has a fusiform shape with a more convex anterior edge. This plate is crossed by a transverse ridge ending at the orbital fenestra (Pl. III fig. 3). Behind the ridge there is a groove parallel to it. The length/breadth ratio in the postpineal plate changed gradually during the growth of the fish (Table 2).

Table 2.

	Length of body (without tail) cm	Postpineal plate		Length/breadth ratio of postpineal plate
		length mm	breadth mm	
Juvenile *Asterolepis*	1.48	0.9	2.8	0.32
	2.6 approx.	1.8	3.9	0.46
	3.8 approx.	2.5	5.0	0.50
Adult *Asterolepis ornata*	33.2	19.0	33.0	0.57

The orbital fenestra, as compared to that of adult *Asterolepis*, occupies a considerably larger area of the head-shield. Its anterior edge is almost straight, the posterior one is concave. Orbital walls are formed by narrow high ridges on the medial edge of the lateral plates and the posterior edge of the praemedial plate (Pl. II fig. 1). The bones situated in the orbital fenestra are often deformed. The pineal plate, as compared to that of adult *Asterolepis ornata*, is more convex. Its corners are tapered (Pl. III fig. 4). The postpineal and lateral plates overlap the posterior edge of pineal plate and the rostral plate the anterior edge of this plate. The sclerotic bones are convex and covered with reticular ornament. The bones of the visceral skeleton (Pl. II fig. 3,4) will not be discussed in the present paper.



Text-fig. 3. A - reconstruction of adult *Asterolepis ornata*, ventral view (after Lyarskaya, 1981); B - reconstruction of juvenile *Asterolepis*, ventral view, chiefly after 260/87 a. AVL - anterior ventrolateral, PVL - posterior ventrolateral, MV - median ventral, SM - submarginal, Sm - semilunar, SO - suborbital plates, vlr - ventrolateral ridge of trunk armour, sar - subanal ridge, scr 1 - subcephalic ridge 1, scr 2 - subcephalic ridge 2 (abbreviations in Text-figs. 2 and 3 after Hemmings, 1978 and Young, 1984).

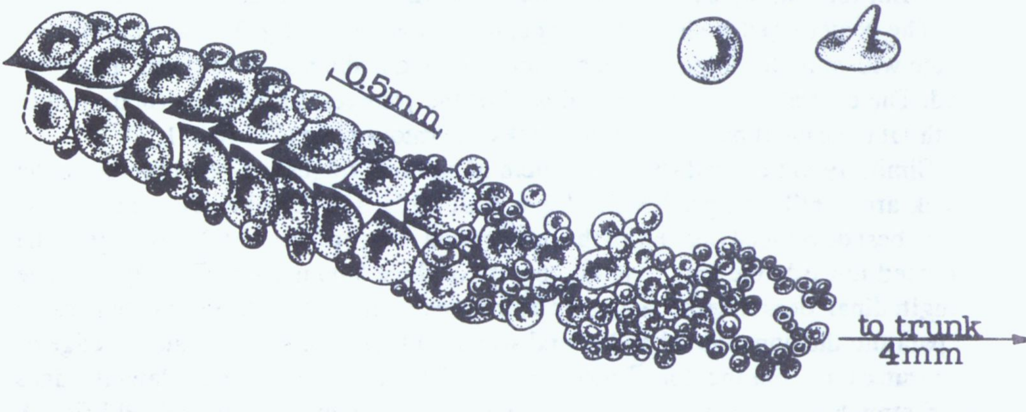
The **trunk-shield** of young individuals (Text-figs. 2,3) consists of five walls: two dorsolateral and two lateral walls and a ventral wall. The dorsolateral walls form probably an angle of about 130°. Along the lateral walls runs the longitudinal main lateral line groove, as in adult *Asterolepis*. The ventral wall is longer than the dorsolateral walls. It consists of the anterior (subcephalic), the principal and the posterior (subanal) parts. The anterolateral corners are well developed (Pl. II fig. 4). The posterior edge shows two angular processes (Pl. I fig. 3). The ventral wall is the widest in the anterior subcephalic part, and is the narrowest in the posterior end. The central part of the ventral wall of the youngest individuals (body length without the caudal part 1.1-1.3 cm) lacks an armour plate (Pl.I figs. 1, 3).

Similarly to the head shield a system of external ridges can be observed in the trunk-armour (Text-figs. 2, 3; Pl.I fig. 6, Pl.II fig 5). The dorsal median ridge (dmr) is the best developed one. From the ossification centre of the AMD two ridges (otr) proceed towards the anterolateral corners of dorsolateral walls (Pl.I fig. 6). The longitudinal dorsolateral ridges (dlr) run parallel to the dorsal median ridge separating the dorsolateral and lateral walls (Pl.II fig. 5). At the posterior edge of the trunk they join the dorsal median ridge. The longitudinal ventrolateral ridges (vlr) stretch along the junction of the lateral walls and the ventral wall (Pl.I fig. 3). In the anterior and posterior parts of the ventral wall they fuse, thus separating the subcephalic and subanal parts from the rest of the wall. From them subanal ridges (sar) branch out at the posterior end of the wall (Pl.I fig. 3). In the anterior part of the wall less pronounced subcephalic ridges occur (Text-fig. 3, scr1, scr2). In the posterior part of the trunk-shield the dorsolateral and ventrolateral ridges are connected by means of short transverse ridges situated on the PDL (Pl.II fig. 5).

In the juveniles the visceral side of the trunk-shield carries the anterior and posterior transverse ridges. The anterior ridge is the most clearly pronounced in the corners between the ventral and lateral walls where it forms a lamina, and is more weakly expressed between the dorsolateral and lateral walls (Pl.II fig. 3). The posterior transverse ridge is situated behind the external transverse ridges and is more prominent on the dorsal side. The anterior part of the AMD shows a roughened area, probably representing the attachment area of *musculus levator capitis* (cf. adult *Asterolepis estonica*; Karatajūte-Talimaa, 1963, Pl.I fig. 2-4). On the visceral side of the PMD the posterior ventral pit, pt2 (Pl.II fig. 4; Pl.IV fig. 7) occurs at the posterior transverse ridge (cf. Karatajūte-Talimaa, 1963, Pl.I fig. 7).

The **pectoral fins** which consist of the proximal and distal segments (Pl.I fig. 5; Pl.III fig. 2) almost reach the posterior end of the trunk-shield (Pl.I figs. 3,4; Pl.III fig. 2). The length of the pectoral fins varies from 7.6 to 10.9 in the youngest individuals, and is 15 mm in an older juvenile (the only specimen). The length of the distal segment, in contrast to that in adult *Asterolepis ornata*, is greater than the length of the proximal segment; their ratio is 0.57-0.88, but with the growth of the fish they tended to become more uniform in their length. In the older juvenile just indicated the ratio is 0.9. The width of the proximal segment (1.0-1.7 mm) is almost constant. Unlike adult *Asterolepis ornata*, the young individuals had two dorsal central plates and probably also two ventral central plates in the distal segment.

The medial and lateral edges of the pectoral fin bear elongated denticles which, in contrast to those in adults, are longer and more sparse (Pl.I fig.3). The distal end of the fin is very sharp. The bones of the fin segments suture by means of minute sharp spines.



Text-fig. 4. Squamation of the caudal part of a juvenile in visceral view, separate scales in external view (after specimen 260/9).

The **caudal part** of young *Asterolepis* comprises about half of the fish length (Pl.I fig. 2). The tail is heterocercal (Pl.IV fig. 4). The dorsal fin lies not far from the posterior margin of the trunk shield (Pl.IV figs. 4,5). The caudal part is covered with scales resembling tubercles of some early vertebrates. In their central part the scales have a tubercle on the external side and a cavity or pulpar opening on the visceral side. The tubercle is conical (height up to 0.25 mm) and its tip is turned posteriorly. The scale base is circular, sometimes oval, its diametre being 0.07 to 0.20 mm. The scales were situated in longitudinal and perpendicular rows and overlapped each other. The diametre of the pulpar opening is variable. On the lower surface of the caudal part in the central row some scales have a cavity that occupies the whole base. The scales differ in size depending on their age and position in the squamation (Pl.IV fig.1). Between large scales there sometimes occur very small ones with rather pronounced tubercles. On the dorsal side of the caudal part, starting from its posterior second half, two rows of alternating large scales occur; here the scale bases are of a tapered elongated configuration (Text-fig. 4; Pl.IV figs. 2,3).

The internal anatomy. In 64 juveniles an inclusion is found that, probably, represents their stomach content (for comparison see Denison, 1941). It is always situated in the anterior part of the left side of the trunk and consists of dark dense substance covered with lighter and looser substance. Similar composition is found in coprolites occurring in the same layer. The inclusion is elongated and oriented lengthwise the body (Pl.I fig. 2; Pl.II fig. 3). The width/length ratio is about 0.4.

The ornament of the armour in juveniles differs considerably from that of adult *Asterolepis*. In smaller juveniles it is somewhat simpler than in the larger ones. In the mediandorsal trunk plates and in the posterior part of the head the most complicated ornament can be observed, whereas in the central part of the ventral wall it is the least developed, e.g. in the MV and along the adjacent edges of the AVL and PVL. A reticular ornament is typical of the smaller juveniles (Pl.III figs. 1,8). Then tubercles and radial ridges appeared, e.g. in the AMD and ADL, as well as on the head shield (Pl.II fig. 1). At the early stages the tubercles were small, rather high and sometimes spine-like. Gradually the radial ornament disappeared, except at armour plate margins, the tubercles became larger in diameter and flatter and the ornament turned into that of adult *Asterolepis*.

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Plate I

Juveniles of antiarch *Asterolepis*, Lode (Liepa) quarry, Latvia; Upper Devonian, Lower Frasnian, Gauja Stage.

Fig. 1. Ventral view; individual is ripped up along bedding plane of rock. x 4, specimen 260/7a, b; Latvian Nature Museum, Riga.

Fig. 2. Ventral view; with the oval inclusion (St), probably, the stomach content. x 4, 260/2a.

Fig. 3. Ventral view with separate armour plates in dorsal view. x 4, 260/87a.

Fig. 4. Dorsal armour in visceral view with the imprint of the stomach (?) content on the left side. The head and anterior part of the trunk (ventral wall), in external view. x 4, 260/24a.

Fig. 5. Ventral view, in the posterior part of the specimen the dorsal armour in exposed in visceral view. A crossopterygian (?) scale lies on the right side; pr.s - proximal segment, d.s - distal segment. x 4, 260/90.

Fig. 6. Dorsal armour in visceral view; dmr - dorsal median ridge of trunk-armour, otr - oblique transverse ridge. x 4, 260/26a.

Plate II

Juveniles of antiarch *Asterolepis*, Lode quarry, Latvia; Upper Devonian, Lower Frasnian.

Fig. 1. Dorsal view of an incomplete older juvenile; the SM shows reticular ornament, the right ADL and the edges of the AMD bear ridges and the central parts of the AMD and Nu carry tubercles. x 4, 260/78, Latvian Nature Museum, Riga.

Fig. 1a. Anterior part of the left SM. x 8, 260/78.

Fig. 2. Dorsal side in visceral view. x 4, 260/4a.

Fig. 3. Ventral view, suborbital plates (SO) and a part of the dorsal armour in visceral view. The right side shows the probable stomach content (St); vtr - visceral transverse ridge; t - terminal, Sm - semilunar plates. x 4, 260/1a.

Fig. 4. Anterior part of the individual in ventral view, the La and PNu are in dorsal view, the SO in visceral view. Posterior part shows the dorsal armour in visceral view. pt2 - posterior ventral pit. x 4, 260/25a.

Fig. 5. Visceral view; the individual is split into part and counterpart; PDL - posterior dorsolateral plate, dlr - dorsolateral ridge of trunk-armour. x 4, 260/13a, b.

Plate III

Juveniles of antiarch *Asterolepis*, Lode quarry, Latvia; Upper Devonian, Lower Frasnian.

Fig. 1. Reticular ornament on the PMD. x 20, 260/88a, Latvian Nature Museum, Riga.

Fig. 2. Dorsal armour in visceral view; pr.s - proximal segment, d.s - distal segment. x 4, 260/12a.

Fig. 3. Dorsal view of the head-shield; Nu - nuchal, PNu - paranuchal, La - lateral, SM - submarginal plates. x 8, 260/5a.

Fig. 4. Orbital fenestra in visceral view; R - rostral, Pi - pineal plates. x 15, 260/82a.

Fig. 5. Left ADL in external view. x 4, 260/252a.

Fig. 6. Right SM plate in external view. x 4, 260/253a.

Fig. 7. AMD in external view. x 4, 260/254.

Fig. 8. Right PVL in external view. x 4, 260/255.

Fig. 9. Right AVL in visceral view. x 4, 260/251a.

Plate IV

Juveniles of antiarch *Asterolepis*, Lode quarry, Latvia; Upper Devonian, Lower Frasnian.

Fig. 1. Squamation of the caudal part behind the trunk-armour. Arrow points to the end of the tail. x 18, 260/25a, Latvian Nature Museum, Riga.

Fig. 2. The end of the tail and some isolated scales. x 18, 260/25a.

Fig. 3. Caudal part; in a number of scales the bases are of tapered elongated shape. Arrow points to the end of tail. x 20, 260/9.

Fig. 4. Complete caudal part with the dorsal fin. x 6, 260/80a.

Fig. 5. Dorsal fin. x 15, 260/80a.

Fig. 6. Posterior part of the trunk-armour showing the external ridge system, dorsal view. x 4, 260/41.

Fig. 7. PMD with the posterior ventral pit (pt2), visceral view. x 15, 260/25a.

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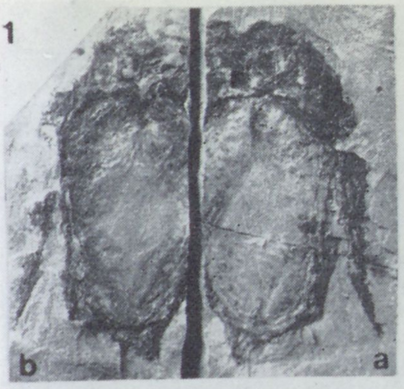

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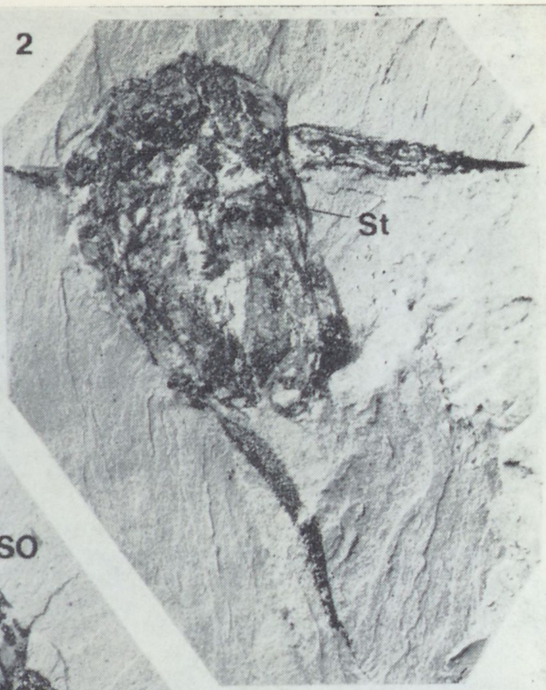

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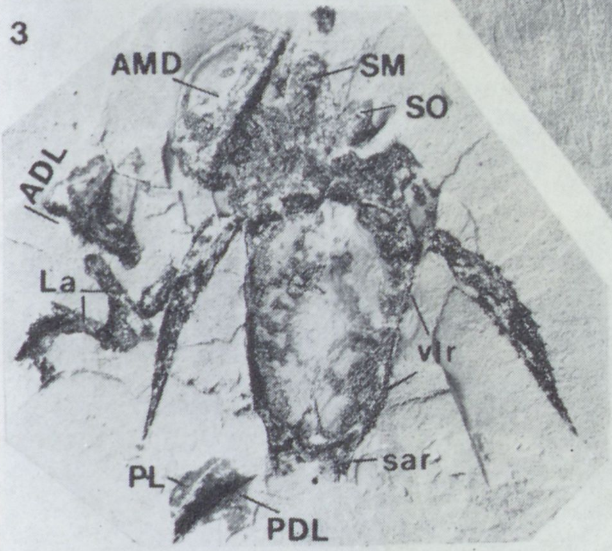

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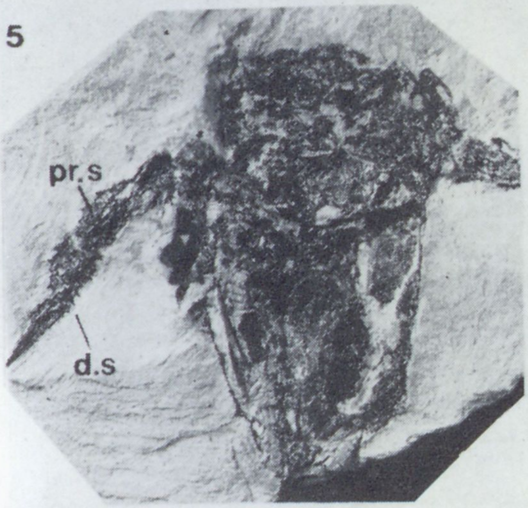

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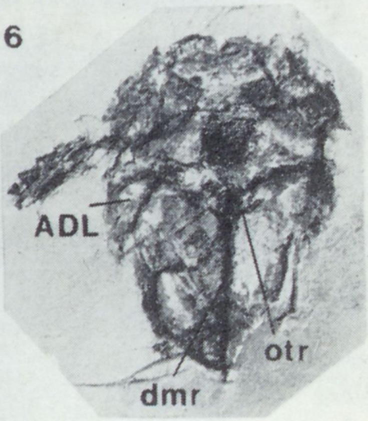

Plate II

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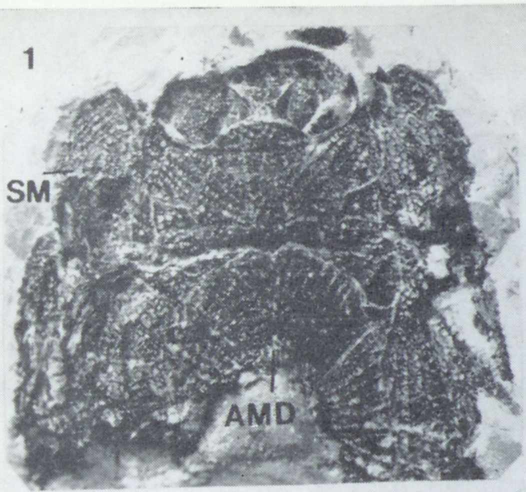

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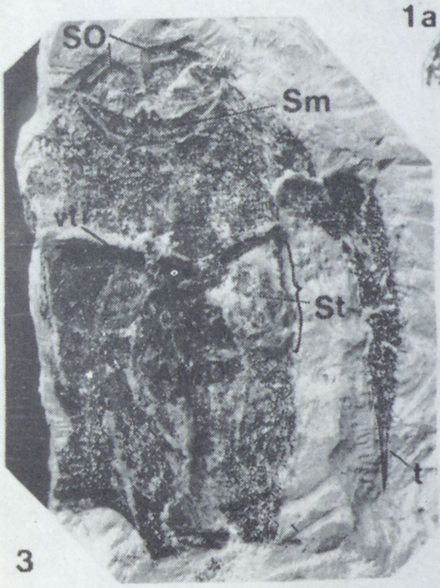

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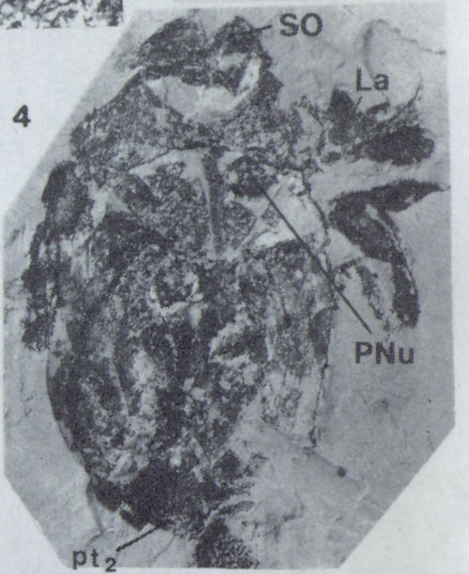

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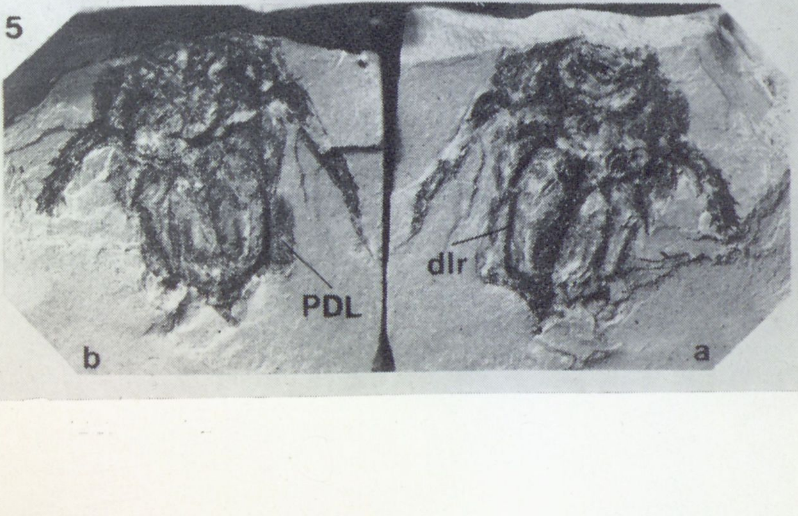

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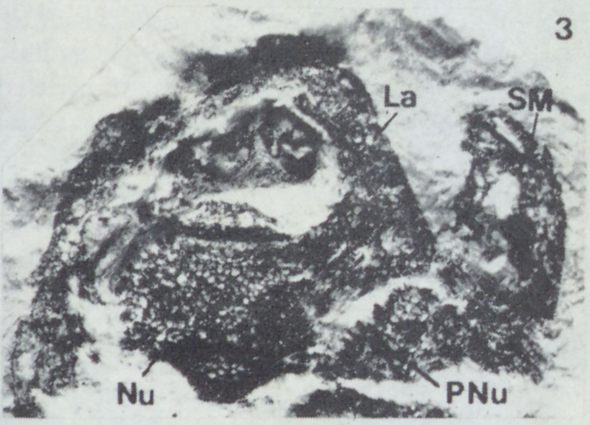
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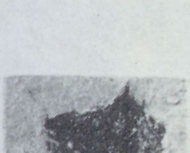
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Plate IV

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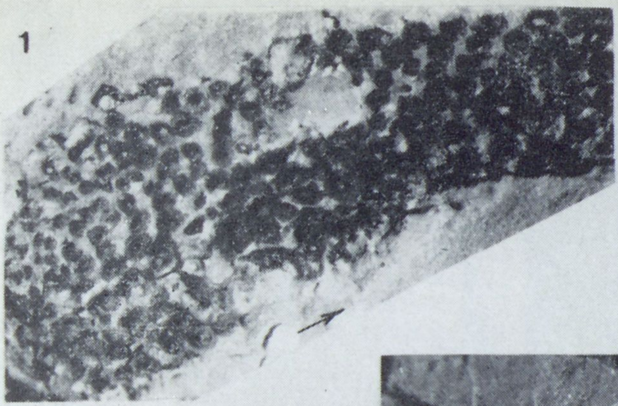

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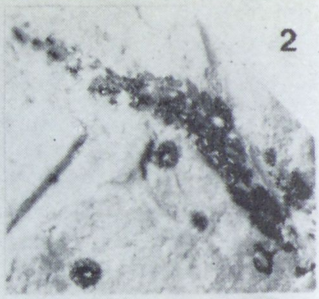

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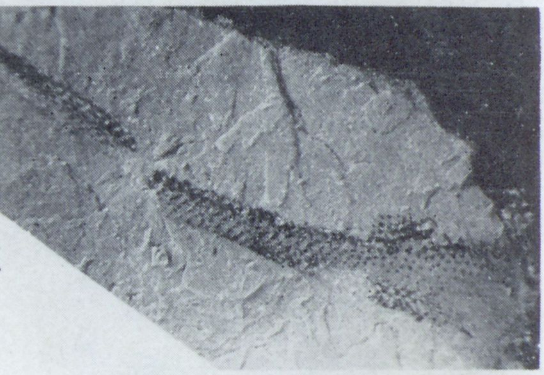

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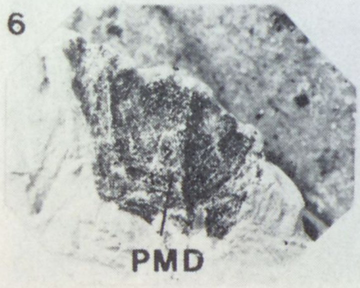

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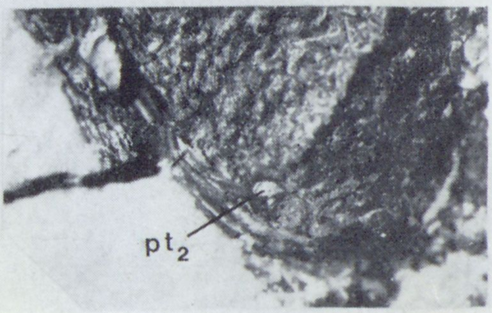

New Middle Devonian antiarchs (Placodermi) of Central Kazakhstan

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Abstract. Two species of the genus *Bothriolepis* (family Bothriolepididae): *B. kassini* Malin. and *B. babichevi* sp.n. are described. A new species of the genus *Tenizolepis*, *T. bychkovi* has also been established. Antiarch remains have been collected from the Trudovoe locality situated on the right bank of the Shiderti River, to the north of Karaganda in the north-eastern part of Central Kazakhstan. Stratigraphically the locality belongs to the Konyr Formation, and lies under a sedimentary rock unit containing plant remains of Givetian age.

Six antiarch localities (Text-fig.1) are known from the Devonian of the Olenti and Shiderti River basins lying north of Karaganda. Antiarchs from the Amankonyr, Krasnyj Pakhar' and Saumalkol' localities belong to four recently described species of the genus *Bothriolepis* (Malinovskaya, 1988). The systematic composition of antiarchs from the Shybyndy locality cannot be established due to scarcity of finds and a fragmentary state of fish remains. The present paper concentrates on the results derived from the study of rich antiarch material from the Trudovoe locality. Among the antiarchs from this locality two species of the genus *Bothriolepis* have been identified — the previously known species *B. kassini* Malin. and a new species *B. babichevi*, and also a new species of the genus *Tenizolepis*, *T. bychkovi sp.n.*

The Trudovoe locality is situated on the right bank of the Shiderti River (Text-fig. 1), and is attributed to the Konyr Formation of Givetian age (Text-fig. 2). Impressions of antiarch plates have been recorded from greyish-green sandstones and siltstones of the Lower Konyr Subformation (D_2kn_1), overlain by variegated sandstones of the Upper Konyr Subformation (D_2kn_2), containing impressions of Givetian plants *Lepidodendropsis* sp., *Barrandeina orlovii* Jur. and *Pseudosporochnus nodosus* Lecl. et Banks.

The genus *Bothriolepis* is widespread in the Middle and, particularly, in the Late Devonian rocks throughout the world. At present, more than 90 forms of this genus are known (Malinovskaya, 1988; Young, 1988). In Central Kazakhstan representatives of the genus *Bothriolepis* were first found in the Frasnian rocks together with fossil plants. They served as a reliable mark of the base of the Frasnian Stage in this region. With the occurrence of bothriolepids in the Givetian, the stratigraphical range of *B. kassini* Malin. (Givetian- Frasnian) and, thus, of the whole genus *Bothriolepis* widened in Central Kazakhstan.

The genus *Tenizolepis* was earlier known only from the Givetian of West Central Kazakhstan (Malinovskaya, 1977), being represented by two species: *T. rara* Malin.

and *T. asiatica* (O.Obr.). As *T. bychkovi* sp.n. occurs in the Givetian Konyr Formation, the geographical range of this genus has widened in Central Kazakhstan and its Givetian age has been confirmed.

Family Bothriolepididae Cope, 1886

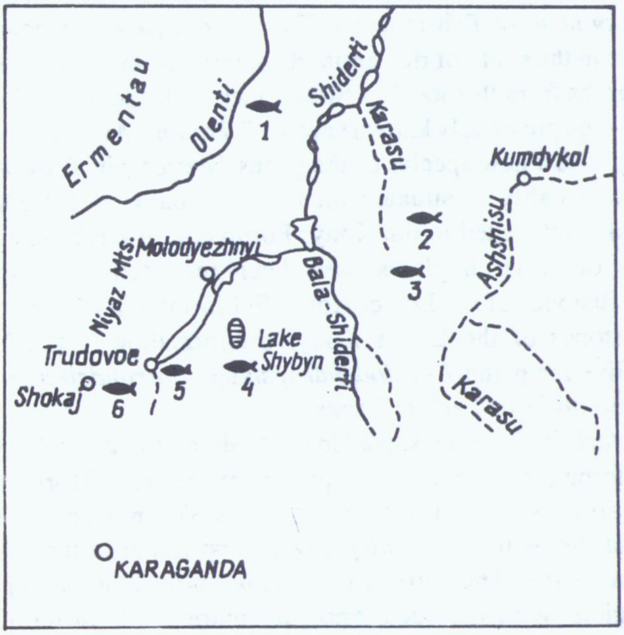
Bothriolepis Eichwald, 1840

Bothriolepis kassini Malinovskaja, 1988

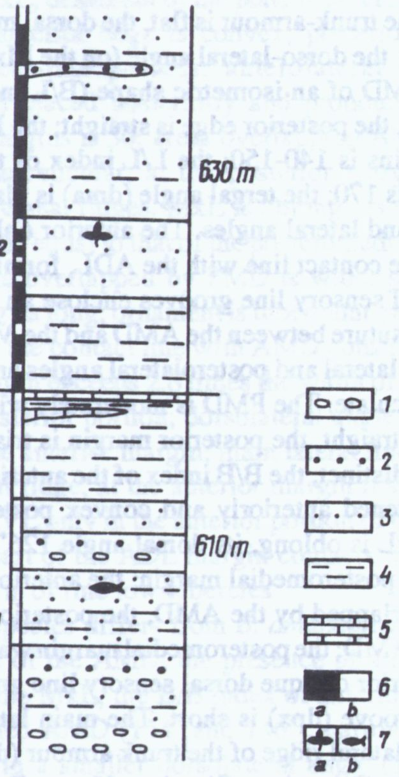
Pl.I figs. 1,2,4,5,7,8; Text-fig. 3

B. kassini: Malinovskaya, 1988, p.62-63, Pl.I, figs. 6-9; Figs. 2,3.

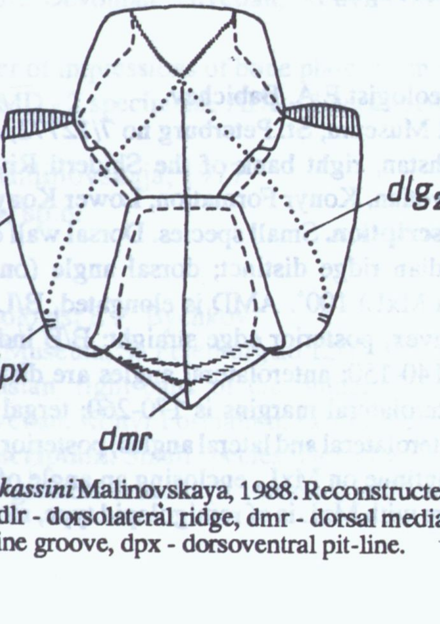
Description. The L is wide and short, its B/L index is 70; the orbital margin is moderately concave; the margin in contact with PrM in length exceeds twice the edge, making contact with the Nu; the anterior edge is wide, moderately convex; the lateral margin is concave; the margin in contact with the PMg is short and straight, the lateral portion of the plate is much narrower than the mesial one; the central sensory line groove (csl) reaches the semicircular pit-line groove (cir).



Text-fig. 1. Antiarch localities in the north-eastern part of Central Kazakhstan: 1 - Amankonyr, 2 - Krasnyj Pakhar', 3 - Saumalkol', 4 - Shybyndy, 5 - Trudovoe, 6 - Shokaj.



Text-fig. 2. Section of the Konyr Formation at the Trudovoe village (after data of T.M. Kodrul): 1 - conglomerate, 2 - gravelstone, 3 - sandstone, 4 - siltstone, 5 - limestone; 6 - colour of rocks: red (a), green (b); 7 - remains of fossil plants (a) and antiarchs (b).



Text-fig. 3. *Bothriolepis kassini* Malinovskaya, 1988. Reconstructed dorsal wall of the trunk armour. Abbreviations: dlr - dorsolateral ridge, dmr - dorsal median ridge, dlg2 - posterior oblique dorsal sensory line groove, dpx - dorsoventral pit-line.

The dorsal wall of the trunk-armour is flat, the dorsal median ridge is indistinct; the dorsal angle is 148°; the dorso-lateral angle (on the MxL) 23°, the length of the wall is 65 mm. The AMD of an isometric shape (B/L index 90) is flattened; the anterior edge is convex, the posterior edge is straight; the B/B index of the anterior and the posterior margins is 140-150; the L/L index of the anterolateral and the posterolateral margins is 170; the tergal angle (dma) is placed at an equal distance from the anterolateral and lateral angles. The anterior oblique dorsal sensory line grooves (dlg_1) reach the contact line with the ADL, forming an angle of 131°; the posterior oblique dorsal sensory line grooves enclose an angle of 73°. The AMD overlaps the ADL. The suture between the AMD and the MxL is of the remigolepid type. The anterolateral, lateral and posterolateral angles are distinct. The ornament of the plate is fine- reticulate. The PMD is moderately wide, its B/L index is 111; the anterior margin is straight, the posterior margin is triangular; the anterior and dorsolateral angles are distinct; the B/B index of the anterior and posterior margins is 50; the plate is flattened anteriorly and convex posteriorly; the ornament is fine-reticulate. The MxL is oblong, its dorsal angle 126°; the mesial edge of the plate is shorter than the posteromedial margin; the anterior (shorter) portion of the mesial margin was overlapped by the AMD, the posterior (longer) portion of the margin overlapped the AMD; the posteromedial margin was completely overlapped by the PMD. The posterior oblique dorsal sensory line groove (dlg_2) is long. The dorsoventral pit-line groove (dpx) is short. The main lateral line groove (lcg) is placed below the dorsolateral ridge of the trunk armour (dlr).

Occurrence. Middle Devonian, Givetian, Konyr Formation; north- east of Central Kazakhstan.

Material. A number of impressions of bone plates from the Trudovoe locality: L - 1 specimen, AMD - 3 specimens, PMD - 1 specimen, MxL - 3 specimens.

Bothriolepis babichevi sp.n.

Pl.I figs.3, 6, 9-11

Name: After the geologist E.A. Babichev.

Holotype. CNIGR Museum, St. Peterburg no 7/12772; anterior median dorsal plate; Central Kazakhstan, right bank of the Shiderti River, Trudovoe village; Middle Devonian, Givetian, Konyr Formation, Lower Konyr Subformation.

Definition and description. Small species. Dorsal wall of the trunk-armour 75 mm long, dorsal median ridge distinct; dorsal angle (on AMD) is 144°-146°, dorsolateral angle (on MxL) 100°. AMD is elongated, B/L index 85-95; anterior margin is slightly convex, posterior edge straight; B/B index of the anterior and posterior margins is 140-150; anterolateral angles are distinct; L/L index of the anterolateral and posterolateral margins is 170-260; tergal angle is placed at the same distance from anterolateral and lateral angles; posterior oblique dorsal sensory line grooves (dlg_2) continue on MxL, enclosing an angle of 70°; area overlapping ADL is wide, the suture with MxL is of remigolepid type, most of the posterolateral edge is overlapped by MxL; ornament of the plate is tubercular- reticulate. PMD is wide, B/L index 130; anterior edge is convex, posterior is triangular, with a posteriorly directed keel-like process; anterolateral angles are indistinct, posterolateral angles are placed posteriorly and pronounced; B/B index of the anterior and posterior margins is 50; areas overlapping AMD and MxL are wide; ornament of the plate is reticular, at the posterior margin fine-tubercular and consisting of short transversal ridges. MxL is oblong, its dorsal angle 120°-134°; length of the mesial edge is equal to that of the posteromedial one; area overlapping AMD is narrow, the one overlapped by PMD is wide; posterior oblique dorsal sensory line groove (dlg2) is long; ornament is tubercular-reticulate, near the suture with PMD tubercular, at the contact line with AMD consists of transversal ridges. ADL is elongated, its length exceeds 2.8 times the width of the plate; lateral lamina is the broadest in the posterior portion; dorsolateral angle is 120° in the posterior portion and 110° near the anterior margin; main lateral line groove (lcg) is placed nearer to the dorsolateral ridge, at the anterior margin it sharply curves upwards. ADL is overlapped by AVL only in the anterior portion of the plate, the overlapped area is wide; posterior part of the ADL margin contacts with a part of the medial edge of AVL; ornament is of fine low tubercles.

Comparison. New species differs from *B. amanconyrica* in a smaller size of the trunk armour, shape of the AMD, the presence of a remigolepid-type suture between the AMD and the MxL, the B/B index of anterior and posterior margins (180-95), a more flattened AMD (154° and 146°), narrow and elongate PMD. It differs from *B. kassini* in a smaller dorsolateral angle (123° and 100°), lack of anterior oblique dorsal sensory line grooves on the AMD, the shape of the posterior margin of the PMD and shape of the MxL. From the *B. nikitinae* it differs in the shape of the AMD, the remigolepid suture of the AMD and the MxL, and from *B. tastenica* in the elongated shape of the AMD and the PMD, and a shorter and wider MxL.

Occurrence. Middle Devonian, Givetian, Konyr Formation; north- east of Central Kazakhstan.

Material. A number of impressions of bone plates from the Trudovoe locality: AMD - 1 specimen, PMD - 2 specimens, ADL - 1 specimen, MxL - 3 specimens.

Genus Tenizolepis Malinovskaja, 1977

Tenizolepis bychkovi sp.n.

Pl.II figs. 1-7

Name: after the geologist E.P. Bychkov.

Holotype. CNIGR Museum, St. Peterburg no 12/12772:, anterior median dorsal plate; Central Kazakhstan, right bank of the Shiderti River, Trudovoe village; Middle Devonian, Givetian, Konyr Formation, Lower Konyr Subformation.

Definition and description. Small species. Dorsal wall of the trunk-armour is about 80 mm long, its greatest breadth (if restored) is 70 mm; dorsal angle of the wall is 150° (on AMD), dorsolateral angle varies from 110° (on MxL) to 135° (on ADL). Ventral wall is flattened, its subcephalic and subcaudal portions are short; length of the wall is 100 mm, breadth 50 mm; ventrolateral angle is 120°-130° (on AVL and PVL). AMD is flattened, elongated; B/L index is 75- 80; anterior margin is convex, posterior straight; B/B index of the anterior and posterior margins is 57; L/L index of the anterolateral and posterolateral margins is 170; anterolateral angles are rounded, indistinct; lateral and posterolateral angles are distinct; tergal angle is placed anteriorly of lateral angles; posterior oblique dorsal sensory line grooves are long, reach the suture with MxL, enclosing an angle of 56°. AMD overlapped ADL with the anterior portion of the anterolateral margin and being overlapped by ADL in the posterior portion of the anterolateral margin; the overlap area is narrow; suture with MxL is of remigolepid-type, the overlap area being wide; ornament is tubercular-reticulate. Anterior margin of PMD is triangular. ADL is of moderate length, B/L index of the dorsal lamina is 50; main lateral line groove (lcg) is placed nearer to the dorsolateral ridge; overlap area with MxL is wide. ADL is overlapped by AVL in its anterior portion, posteriorly the suture is without overlapping. MxL is wide, B/L index of the dorsal lamina is 65; dorsal angle is 120°; L/L index of the mesial and posterior medial margins is 70; main lateral line groove on PDL is placed closer to the dorsolateral ridge; posterior oblique dorsal sensory line groove (dlg2) is lacking. AVL is considerably wide in the subcephalic portion; anterolateral angle (al) is distinct; L/L index of the subcephalic division and the whole AVL is 30; B/L index of the ventral wall is 50; areas overlapping MV and PVL are wide; ornament is fine-tubercular. PVL is relatively wide; B/L index of the ventral wall is 52; L/L index of the subcaudal division and the whole PVL is 35; area overlapping MV is wide; ornament is fine-tubercular. MV is large, oval, elongated; its ornament is fine-tubercular. Semilunare is unpaired.

Comparison. New species differs from *Tenizolepis rara* Malin. in a wider dorsal wall of the trunk-armour (70 mm and 47 mm), a convex and wider anterior margin of the AMD, a long posterior oblique dorsal sensory line groove on the AMD extending to the contact line with the MxL, a remigolepid-type suture between the AMD and the MxL, a wider and shorter PMD. It differs from *T. asiatica* (O. Obr.) in a smaller size of the trunk- armour (length of the ventral wall is 100 mm and 258 mm, respectively), posteriorly placed lateral angles in the AMD, a shorter mesial margin of the MxL, and a fine-tubercular ornament of the ventral wall of the trunk armour.

Occurrence. Middle Devonian, Givetian, Konyr Formation, north- east of Central Kazakhstan.

Material. A number of impressions of bone plates from the type locality: AMD - 1 specimen, ADL - 1 specimen, MxL - 1 specimen, AVL - 2 specimens, PVL - 3 specimens, MV - 3 specimens, and 1 specimen of the ventral wall of the trunk-armour with the right pectoral fin.

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Plate I

Figs. 1, 2, 4, 5, 7, 8. *Bothriolepis kassini* Malin. 1 - laterale, CNIGR Museum, St. Petersburg no 1/12772 (x 1.5); 2 - AMD no 2/12772 (x 1); 4 - PMD no 3/12772 (x 1); 5 - PMD no 4/12772 (x 1); 7 - MxL no 5/12772 (x 1); 8 - MxL no 6/12772 (x 1). Central Kazakhstan, right bank of the Shiderti River, Trudovoe village; Middle Devonian, Givetian, Konyr Formation, Lower Konyr Subformation.

Figs. 3, 6, 9-11. *Bothriolepis babichevi* sp.n. 3 - AMD (holotype), CNIGR Museum, St. Petersburg no 7/12772 (x 1); 6 - PMD no 8/12772 (x 1); 9 - MxL no 9/12772 (x 1); 10 - MxL no 10/12772 (x 1); 11 - ADL no 11/12772 (x 1). Central Kazakhstan, right bank of the Shiderti River, Trudovoe village; Middle Devonian, Givetian, Konyr Formation, Lower Konyr Subformation.

Plate II

Figs. 1-7. *Tenizolepis bychkovi* sp.n. 1 - AMD (holotype), CNIGR Museum, St. Petersburg no 12/12772 (x 1); 2 - MxL no 13/12772 (x 1); 3 - ADL no 14/12772 (x 1); 4 - PVL no 16/12772 (x 1); 5 - AVL no 15/12772 (x 1); 6 - MV no 17/12772 (x 1); ventral wall of trunk armour with right pectoral fin, no 18/12772 (x 0.8). Central Kazakhstan, right bank of the Shiderti River, Trudovoe village; Middle Devonian, Givetian, Konyr Formation, Lower Konyr Subformation.

Plate I


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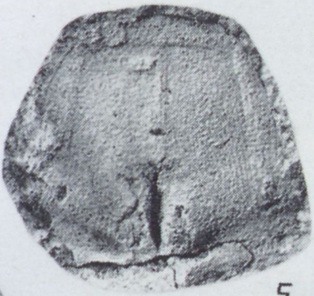
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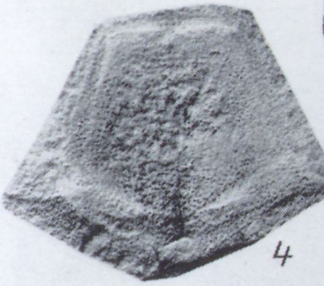
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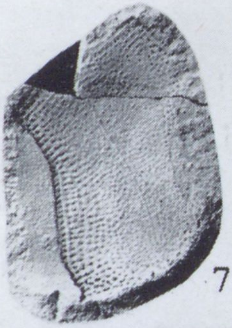
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Plate II

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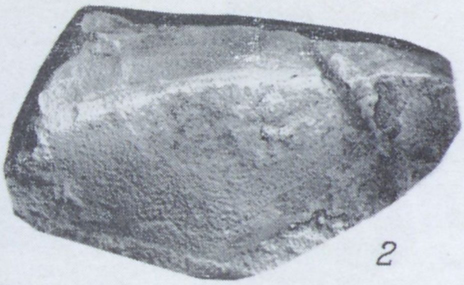

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New remigolepids and high armoured antiarchs of Kirgizia

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Abstract. Previously only one antiarch species, *Bothriolepis turanica* Obr. was known from the territory of Kirgizia. In 1965 and 1982, two new antiarch localities were discovered on the slopes of the Kirgizian Mountain Range. On the northern slope in the Taldybulak Formation, shield remains of a high armoured antiarch *Kirgisolepis karabaltaensis* gen. et sp.n. have been found. This form is assigned by us to the family? Bothriolepididae of the order Asterolepidida (see Obruchev, 1964).

The exoskeleton of *Kirgisolepis* shows co-occurrence of the features characterizing both asterolepiform and bothriolepiform antiarchs, i.e. the sensory groove system is of the bothriolepid, the proportions of the nuchale and its contact with the other skull-roof plates are of the asterolepid, the position of the posterolateral angles, however, is of the intermediate type. The posterior half of the AMD bears a high keel-like ridge.

On the southern slope of the Kirgizian Mountain Range in the upper subformation of the Torsuj Formation, shield fragments of two new species of *Remigolepis*, *R. suusamyrensis* and *R. karakoliensis* were recorded together with the remains of the fossil plant *Leptophloeum* cf. *rhombicum* Dawson.

The paper presents reconstructions of the trunk-shield and skull- roof of *K. karabaltaensis* gen. et sp.n., and as well as the reconstructions of the dorsal wall of the trunk-shield and partly of the skull-roof of both new *Remigolepis* species.

The first information about antiarchs from the territory of Kirgizia dates from the thirties. A single mixilateral bone was discovered by A.A. Denisjuk in 1935 in the sandstone and conglomerate formation along the Kok-Su River, described as *Bothriolepis turanica* by Obruchev (1939). In 1965 V.A. Grishchenko recorded fossils found on the northern slope of the Kirgizian Mountain Range in conglomerates with marl, siltstone and sandstone lenses. According to Obruchev's identification, these fossils belong to antiarchs, namely to a new species of *Bothriolepis* (Grishchenko, 1968). In 1982 S.B. Gushchin repeated investigations on the northern slope, and he also found a new locality of antiarchs on the southern slope of the Kirgizian Mountain Range.

In 1988 we collected material from the same localities, significantly completing the information about Kirgizian antiarchs. The locality on the northern slope of the Kirgizian Range was named Uzunbulak, that on the southern slope Ala-Archa (according to the names of the streams).

Localities with *Remigolepis* are known from eastern Greenland (Stensiö, 1931), Scotland (Andrews, 1978), China (Pan, 1987), Australia (Hills, 1932), Russia (Tula region, locality Andreyevka-2; Lebedev, 1986; Lukševičs, 1991), and Kirgizia (locality Ala-Archa).

The Ala-Archa locality is situated approximately 60 km south of the city of Frunze on the right bank of the Karakol Zapadny River. Fish fossils are found here in two lenses of greenish-grey siltstones in the middle part of the upper subformation of the Torsuj Formation. Vertically the distance between the lenses is about 50 m. In the lower lens the dorsal part of the trunk-shield and some separate poorly preserved plates of *Remigolepis*? have been found. In the upper lens the material is better preserved. The accumulation of fish fossils took place in a thin, 5-15 mm thick layer. Here separate plates of the trunk-shield, several ventral shields and fragments of pectoral fins and skull- roof bones of *Remigolepis* spp. have been found. At the base of this lens and similar greenish-grey siltstone lenses situated upward and downward in the section, the plant fossils *Leptophloeum* cf. *rhombicum* Dawson occur.

In Uzunbulak, the fish fossils have been found in a marly siltstone lens in the middle part of the conglomerate lying in the base of the Taldybulak Formation. They do not form large accumulations. Rarely a few crossopterygian remains can be met with here. The plates of *Kirgisolepis karabaltaensis* gen. et sp.n. predominate. Beside separate plates, several skull-roof fragments and one incomplete head-shield in its natural connection with the fairly complete trunk-armour were found here. The bones belong to fishes of different ages, but the remains of adults predominate.

Order Asterolepida

Family ? Bothriolepididae Cope, 1886.

Genus *Kirgisolepis* Panteleyev, gen.n.

Name is derived from Kirgizia and "lepis" (Greek) - scale.

Type species: *Kirgisolepis karabaltaensis* sp.n.

Diagnosis: The skull-roof is long, trapezium-shaped, posterolateral corner (plc) is slightly displaced anteriorly. Lateral process (lpr) is distinct. Anterolateral corner (alc) is poorly distinguished, and displaced to anterior margin of the skull-roof. Orbital fenestra (Orb) is broad. The posterior ventral wall of praemedial plate (Prm) is slightly concave. Postpineal plate (Pp) borders on the lateral plate(L). Semicircular pit-line groov (cir), vertical (vcp) and central (ifc.b) sensory line grooves are present. Trunk-shield is high. Wedgeform ridge (dmr) extends to posterior median dorsal plate (PMD) on the posterial half of anterior median dorsal plate (AMD). The posterior oblique dorsal sensory line groove (dlg2) is long. Mixilateral plate (MxL) overlaps posterior lateral margin of AMD completely. Anterior dorsolateral plate (ADL) overlaps the AMD posteriorly, but it is overlapped by AMD anteriorly.

Species group: Only type species

Comparison: In the structure of the armour of *Kirgisolepis asterolepiform* and bothriolepiform features are combined. In the structure of the sensory grooves system, the genus resembles the late Devonian genera *Bothriolepis* and *Grossilepis*

(Miles, 1968) which have semicircular, vertical, central, and long posterior oblique dorsal sensory line grooves. Unlike those, the skull-roof of *Kirgisolepis* is not hexagonal, but almost trapezium-shaped. The contact between the postpineal, nuchal (N) and lateral plates is of the asterolepid type. In the structure of the trunk-shield, *Kirgisolepis resembles* the late Devonian *Bothrolepis gippslandiensis* and *B. cullodenensis* from Victoria (Hills, 1931; Long, 1983), but it differs from these forms in the shape of the median dorsal ridge, a long subcephalic part and the absence of the contact between the nuchal plate and orbital fenestra. The structure of suture areas between the AMD and the ADL, as well as the structure of the Pp and L in *Kirgisolepis* is similar to those in *Tenizolepis* from Central Kazakhstan (Malinovskaya, 1977). From the latter it differs in the proportions of the skull-roof, position of preobstantic corners, and a high pointed ridge.

Remarks. Among asterolepiform antiarchs *Kirgisolepis* mostly resembles the Middle Devonian *Byssacanthus* (Karatajūte-Talimaa, 1960) and *Stegolepis* (Malinovskaya, 1973) from the fam. Pterichthyidae. The representatives of these genera have a similar skull-roof form; the cir is present, but the vcp, ifc.b and dlg_2 are absent in these forms. On the AMD there is a ridge with a rounded anterior edge. Besides, the pectoral fins are short and possess a broad distal segment. *Kirgisolepis* has rather long pectoral fins with cogged median dorsal and dorsoventral ridges. The contact between the central dorsal plates 1 and 2 is unknown. The distal segment is small and narrow.

Like the Middle Devonian *Grossaspis* (Lepadolepididae) (Obruchev, 1964), *Kirgisolepis* has a high posterior ridge on the AMD which continues on the PMD. The new genus differs from *Grossaspis* in proportions of the subcephalic part, the absence of the dorsal sensory line groove and the ornament of plates.

In spite of many asterolepid features, especially the proportions and the form of the skull-roof, *Kirgisolepis* has a bothriolepid type system of sensory line grooves, which allowed us to assign this new genus provisionally to the family Bothriolepididae. The question about the taxonomical position of *Kirgisolepis* may be elucidated after a detailed study of the pectoral fins structure.

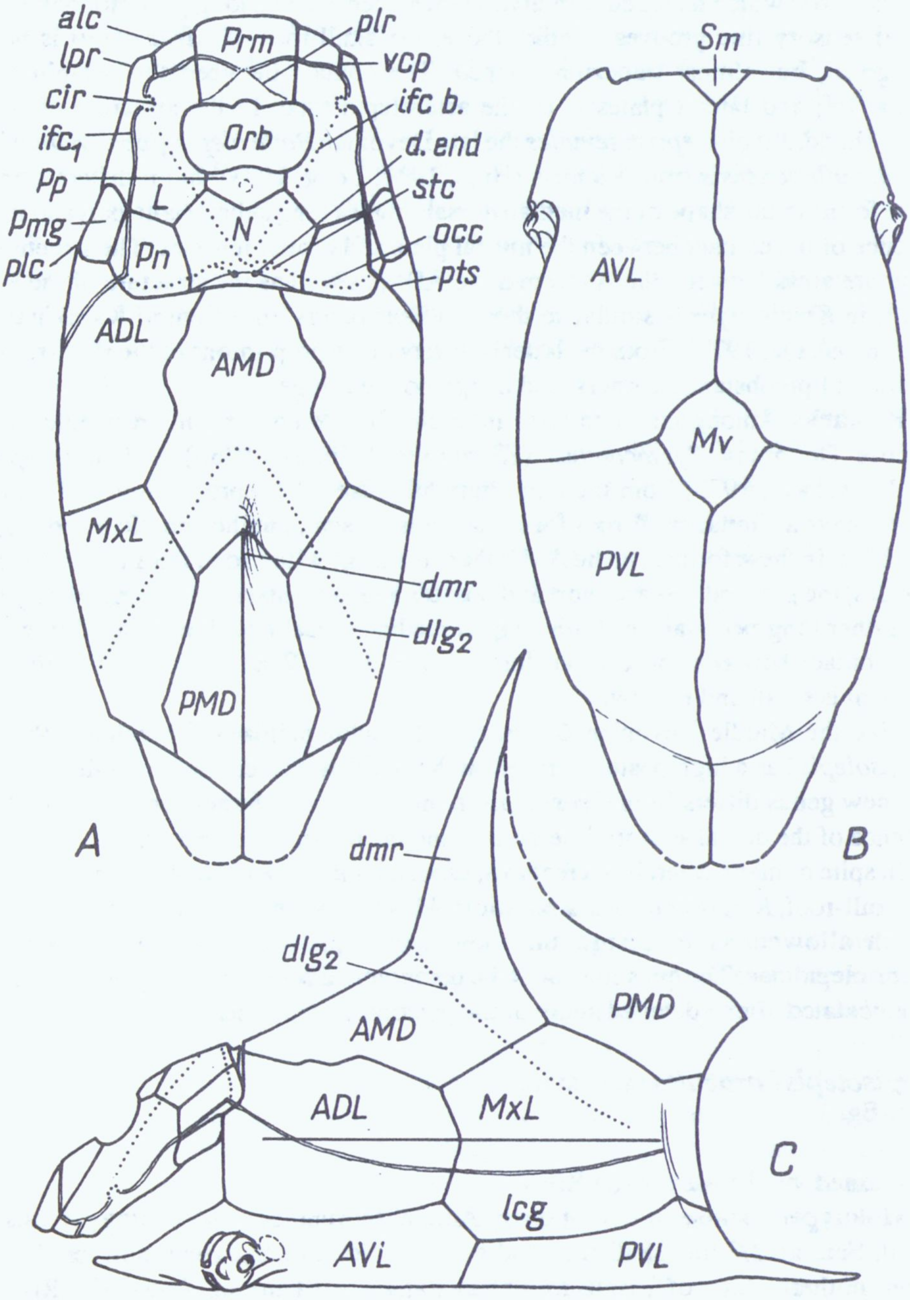
Kirgisolepis karabaltaensis sp.n.

Text-fig. 1

Named by the Kara-Balta River.

Holotype: Institute of Evolutionary Animal Morphology and Ecology Russian Acad. Sci., no 3/3, the skull-roof and trunk-shield in dorsal view; northern Tien Shan, nothern slope of Kirgiz Mountain Range, left bank of Kara-Balta River, mouth region of Uzunbulak stream; Upper Devonian, Taldybulak Formation, lower part of lower subformation.

Diagnosis. Medium sized antiarchs. The skull-roof is 55-60 mm long and 65-70 mm wide. The trunk-shield is 100 mm long in dorsal, and 150-155 mm in ventral side. The infraorbital sensory line (ifc_1) is fused with semicircular pit-line groove



Text-fig. 1. *Kirgisolepis karabaltaensis* gen. et sp. n. Reconstruction of head shield and trunk-armour in dorsal view (A), ventral view (B), and lateral view (C), x 0,65. AVL - anterior ventrolateral plate, PVL - posterior ventrolateral plate, MV - median ventral plate, Sm - semilunar plate, plr - posterolateral ridge, occ - occipital cross-commissural pit-line groove, lcg - main lateral line sensory groove, d.end - external opening of endolymphatic duct. For other explanations see text.

and crosses the posterior margin of the lateral plate between postmarginal (Pmg) and paranuchal (Pn) plates. Dorsal ridge on the AMD is high, wedgeform. The ornament is tubercular.

Material. 59 shield fragments and separate plates: skull-roof and trunk-shield exposed from the external side - 1, fragments of skull-roof - 4, Prm - 3, Pp - 2, L - 2, anterior part of AMD - 1, dorsolateral part of AMD - 1, dmr - 8; fragments: PMD - 1, ADL - 1, MxL - 6, AVL - 10, PVL - 3, MV - 2, proximal segment of pectoral fins - 12, cast of pectoral fin distal segment - 1.

Order Remigolepida

Family Remigolepididae Stensiö, 1931

Genus *Remigolepis* Stensiö, 1931

Remigolepis suusamyrensis sp.n.

Text-fig. 2A

Holotype: Institute of Evolutionary Animal Morphology and Ecology, Russian Acad. Sci., no 4/5, incomplete anterior median dorsal plate in dorsal view; northern Tien Shan, southern slope of Kirgiz Mountain Range, right bank of Karakol Zapadnyj River mouth region of Ala-Archa stream; Upper Devonian, Torsuj Formation, middle part of upper subformation.

Named after the Suusamyr valley.

Diagnosis. Small antiarch with short and broad shields. The width of postpineal and nuchal plates exceeds twice their length. Maximum length of dorsal wall of trunk-shield is 80 mm, its width 70 mm. Subcephalic part is short. Anterior median dorsal plate has round outline with convex anterolateral margins, and tergal angle is slightly displaced anteriorly from the middle of the plate. Angle between anterior oblique dorsal sensory line grooves (dlg_1) is 100°, between posterior ones (dlg_2) 120°-130°. The length of pectoral fins is less than half of dorsal wall of trunk-shield. Denticles of the ventro-median ridge are slightly bent anteriorly.

Comparison. See description of *R. karakoliensis* sp.n.

Material. 36 shield fragments and separate plates: fragments of skull-roof - 2; trunk-shield in dorsal view - 1; trunk-shield in ventral view - 1, AMD - 3, PMD - 6, ADL - 4, PL - 1, AVL - 2, PVL - 2, MV - 1, pectoral fins - 9.

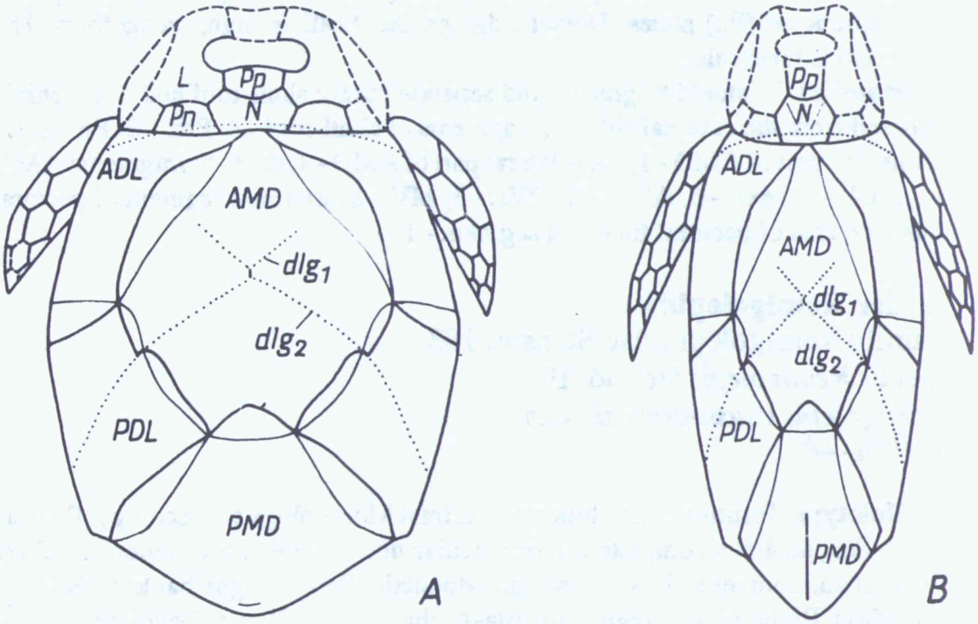
Remigolepis karakoliensis sp. n.

Text-fig. 2B

Holotype: Institute of Evolutionary Animal Morphology and Ecology, Russian Acad. Sci., no 4/8, incomplete anterior median dorsal plate in dorsal view; for locality see *R. suusamyrensis* sp.n.

Named after the Karakol River.

Diagnosis. Small antiarch with narrow long carapace. Postpineal and nuchal plates have nearly equal width and length. The dorsal wall of trunk-shield is 70-90



Text-fig. 2. Reconstruction of head shields and trunk armour of "kirgizian" *Remigolepis* spp. Dorsal view. *R. suusamyrensis* sp. n. (A), *R. karakoliensis* sp. n. (B), x 1. For abbreviations see text.

mm in length, exceeding twice its width. Anterior median dorsal plate has poorly distinguished lateral corners and moderately convex anterolateral margins. Angle between anterior oblique dorsal sensory line is 85°, between posterior ones 95- 100°. Posterior median dorsal plate has pointed anterior margin. The pectoral fins are somewhat longer than half of dorsal wall of trunk-shield.

Comparison. Remigolepids from the Ala-Archa locality resemble the representatives of this genus described by Pan Jiang (1987) from the Zhongning Formation, Ningxia, China in proportions and shape. *R. suusamyrensis* sp.n. similarly to *R. xiangshanensis*, *R. microcephala* and *R. zhongningensis* have short and broad shield, but differs in shorter pectoral fins, a broader posterior margin of the dorsal wall of the trunk-shield and in proportions and shape of overlapping areas of the posterior margin of the AMD. The Ala- Archa remigolepids differ from *R. zhongningensis* also in a shorter anterior part of the AMD and in the absence of the median dorsal ridge situated in its posterior part. From *R. xiangshanensis* they differ in more convex anterior parts of the AMD, and from *R. microcephala* in a more gently expressed lateral corner of the AMD and a shorter postpineal plate.

R. karakoliensis sp.n. is similar to *R. zhongweiensis*, but it differs from the latter in the presense of a narrow pointed anterior margin of the PMD, in the presence of a small median dorsal ridge of the PMD, and in the shape of the remigolepid type of suture.

Material. 50 fragments and separate plates of shields: incomplete trunk-shields in dorsal view - 2, ventral shields - 7, AMD - 15, PMD - 4, ADL - 6, PDL - 2, AVL - 4, N - 1, pectoral fins - 9.

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First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya

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Abstract. *Poracanthodes menneri* sp.n., a new ischnacanthid acanthodian from the Severnaya Zemlya Formation (Lower Devonian, Lochkovian) is described based on articulated specimens. Data of morphological and histological study of jaws, teeth, fin-spines and scales are given. The body of the fish is reconstructed. Finds of complete specimens and the original structure of skeletal elements of *Poracanthodes* exclude the possibility of joining two genera, *Gomphonchus* and *Poracanthodes*.

Introduction

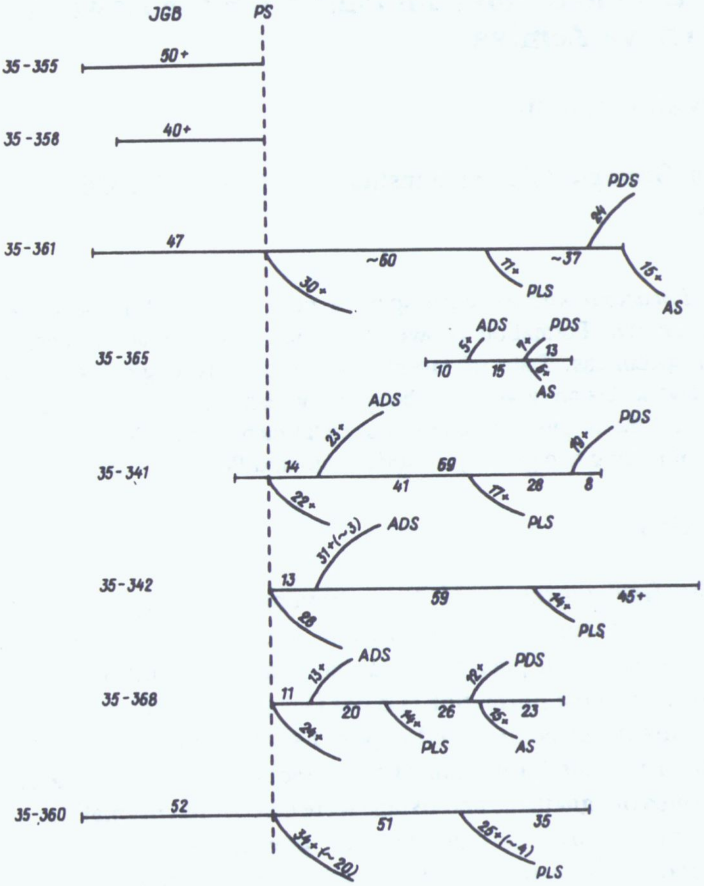
During the field works in 1978 on Severnaya Zemlya Archipelago on the Matusevich, Pod'yomnaya, Spokoinaya, and Ushakov rivers of the October Revolution Island, well preserved acanthodians were collected from the rocks of the Severnaya Zemlya Formation (Lower Devonian, Lochkovian). On these rivers the fish fossils occurred at a well exposed stratigraphical level and denoting the uppermost part of this formation. The acanthodians, as well as the representatives of other groups of agnathans and fishes, were discovered in small (up to 20 cm long) carbonate concretions in thin-bedded dark-grey argillite. The list of fossils of this level (Karatajūte-Talimaa et al., 1986) includes invertebrates — small eurypterids, phyllocarids, ostracodes, also vegetative parts of Charophyta, and vertebrates — anaspids, *Hemicyclaspis* sp.n., *Tesseraspis mosaica* Kar.-Tal., *Corvaspis* sp.n., and acanthodians: Climatiida gen.n., *Nostolepis* cf. *striata* Pander, two new species of nostolepidids, *Nostolepis* sp. no. 6 and *Nostolepis* sp. no. 7, *Cheiracanthoides* sp. no. 4, *Acanthodes* sp.n. and *Poracanthodes menneri* sp.n. (= *Poracanthodes* sp. no. 3 after Valiukevičius, 1988). The latter species is represented rather comprehensively in the collection. The specimens are housed in Lithuanian Research Institute, Vilnius (indices LGMTI coll. no 35).

Family ?Ischnacanthidae Woodward, 1891

Genus *Poracanthodes* Brotzen, 1934

Type species. *Poracanthodes punctatus* Brotzen, 1934. Dittonian erratics (Bey. 36) from the Baltic.

Diagnosis. Scales are rhomboidal, with flat, unornamented crown or ornamented with short parallel or radial ribs on its anterior part. Some concentric grooves and multicuspidate ridges may be observed on the posterior part of the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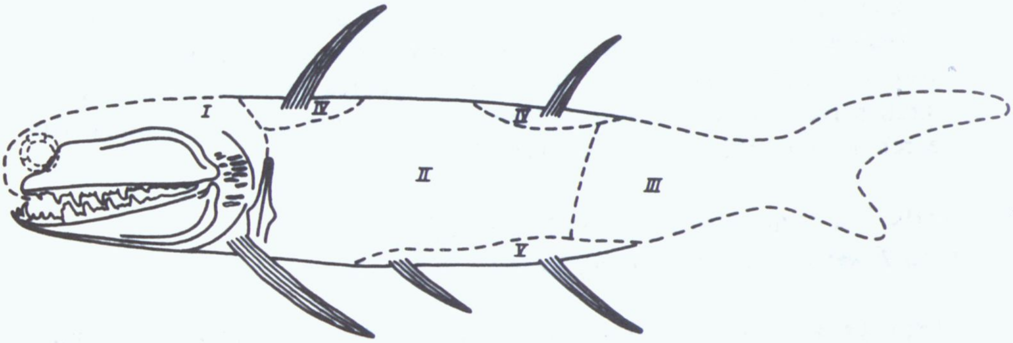
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crown. Pore-canals open on the surface, with numerous pores arranged in radial or concentric lines between the ridges. The crown is composed of dentine and mesodentine, the base of acellular bone or bone with osteocyte cavities. Up to nine principal tooth-cusps with small intercusps occur on each ramus of jaws; the mesial gnathal ridge is provided with denticles. Fin-spines have an enlarged proximal rib and up to nine longitudinal side ribs.

Species. *Poracanthodes punctatus* Brotzen, 1934 and *P. porosus* Brotzen, 1934 from the Baltic Dittonian erratics, *P. gujingensis* Wang, 1989 from the Late Silurian of China, and *P. menneri* sp.n. from the Early Devonian, Lochkovian of Severnaya Zemlya.

Comparison. *Poracanthodes* differs from all the known Ischnacanthidae in having scales with a specific complex pore- canal system. Between *Poracanthodes* and other ischnacanthid genera described on the basis of their fin-spines, jaw-bones or teeth (Denison, 1979), the following differences may be mentioned. The dentigerous jaw-bones of *Acanthodopsis* Hancock and Atthey, 1868 are characterized by a single row with monocuspidate triangular teeth, there is no symphysial whorl, pectoral fin-spines are large and curved. *Atopacanthus* Hussakof and Bryant, 1919 has deeply inserted median spines and teeth lacking small intercusps. In *Persacanthus* Janvier, 1977 jaw-bones bear robust, subpyramidal teeth. *Uraniacanthus* Miles, 1973 has two pairs of intermediate spines. The representatives of *Ischnacanthus* Powrie, 1864 are covered with unornamented small scales; the posterior dorsal fin-spine is larger than the anterior fin-spine and is positioned behind the anal one; the pectoral spines are long and curved. All the spines have four smooth ribs. *Gomphonchus* Gross, 1971 differs in slender, nearly straight fin-spines; its scales are smooth or with radial ridges; the crown is composed of dentine and enameloid, its base is of acellular bone.

Poracanthodes menneri sp.n.

Plates I - X, Text-figs. 1 - 12
1988. *Poracanthodes* sp. no. 3. Valiukevičius, p. 604, Pl. 2.

Etymology. In honour of Dr. Vladimir Menner, Moscow.

Diagnosis. A *Poracanthodes* species with scales that have a flat, rhomboidal crown, a high neck and a large convex base. Up to eight concentric grooves are arranged parallel to the posterior edge of the crown. There are four radial rows with pore-canal openings. The crown bears up to ten growth lamellae of the areal type. The base of the scales is composed of acellular bone. The head plates have large

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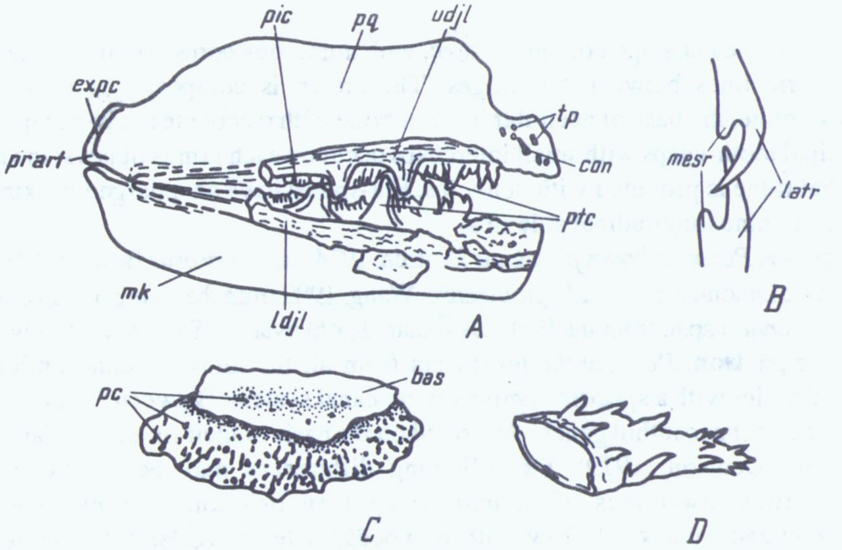
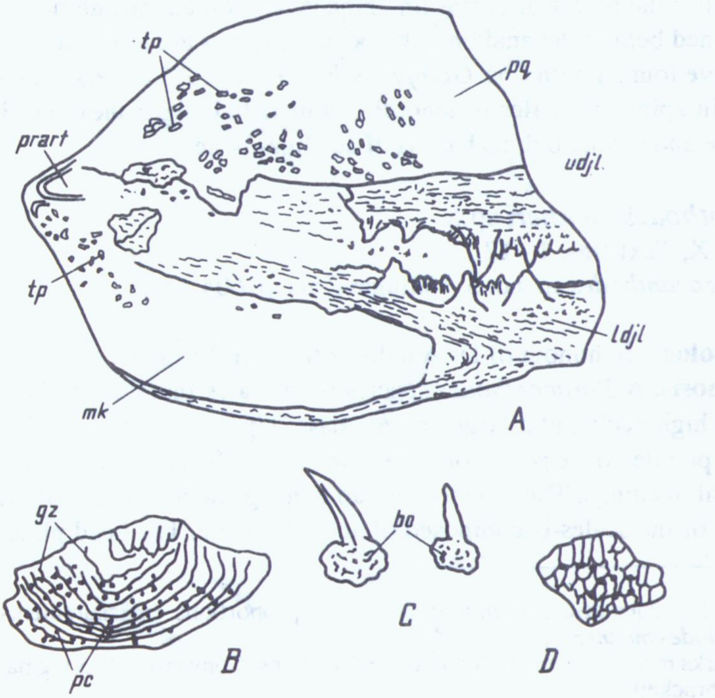
Text-fig. 1. Schematic presentation of body proportions (measurements in mm) in *Poracanthodes menneri* sp.n.
Sign + marks measurements of incomplete fin-spines. Conjectural lacking part of spines is shown in brackets.
Abbreviations used in Text-figures see in p. 211.

Text-fig. 2. *Poracanthodes menneri* sp.n., reconstruction of the adult fish in lateral view. Shape of anterior part of head and tail, conjectural. I-V areas of squamation.



Text-fig. 3. A - left palatoquadrate, meckelian cartilage and articulated lower and upper jaw-bones with teeth of main tooth row, in lateral view. Paratype, LGMTI 35-358 (Pl. II fig. 1), x 3; B - diagrammatic transverse section illustrating the interlocking of the principal tooth-cusps of opposing jaw-bones; C - tessera-like ornamented plate (tp) of the same specimen; D - cone (con) of dentition or branchial apparatus of the same specimen. C and D - x 40.



Text-fig. 4. A - left palatoquadrate, meckelian cartilage and articulated lower and upper jaw-bones with teeth of main tooth row, in mesial view. Paratype, LGMTI 35-355 (Pl. IV fig. 1), x 3; B and D - tessera-like ornamented plates (tp) covering the head, x 40; C - small palatine teeth disposed between the opposing main tooth rows in this specimen, x 50.

osteocyte cavities. The mesodentine in the crown has ascending and multibranched radial vascular canals containing numerous tubules. A complex concentric arcade and 4-6 radial and superficial pore-canals occur as well.

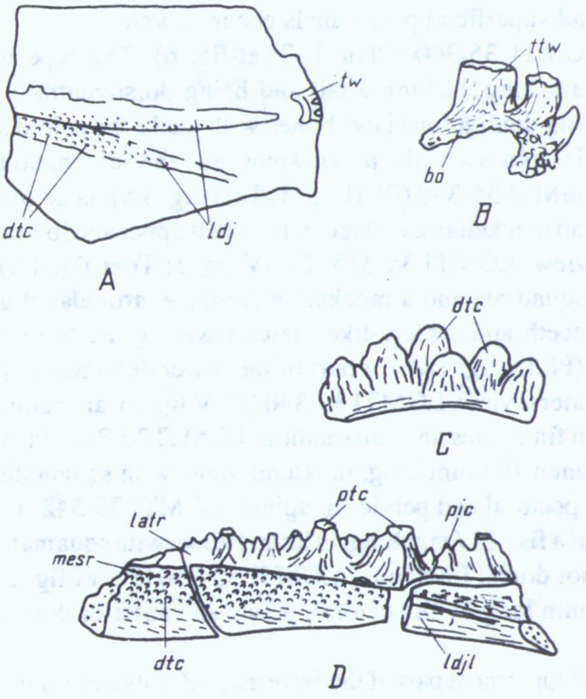
Holotype. LGMTI 35-360 (Plate I; Text-fig. 6). The type is an articulated specimen, 138 mm long, lacking a tail and being dorsoventrally compressed. It shows the opposing dentigerous jaw- bones with teeth, the paired shoulder-girdle, paired pectoral fin-spines and the pelvic spine, and the squamation.

Paratypes. LGMTI 35-358 (Pl. II fig. 1, Text-fig. 3A): head of a fish with a left palatoquadrate and meckelian cartilage, articulated upper and lower jaw-bones with teeth, in lateral view. LGMTI 35-355 (Pl. IV fig. 1; Text-fig. 4A): head of a fish with a left palatoquadrate and a meckelian cartilage, articulated upper and lower jaw-bones with teeth and tessera-like plates covering the head, in lateral view. LGMTI 35-354 (Pl. III fig. 1a,b): a part of the lower dentigerous jaw-bone with a tooth- whorl, in lateral view. LGMTI 35-340 (Pl. V fig. 2): an incomplete specimen, 83 mm long, with fin-spines and squamation. LGMTI 35-341 (Pl. VII fig. 1a,b): an articulated specimen 103 mm long, in lateral view, with squamation, anterior and posterior dorsal, pectoral and pelvic fin-spines. LGMTI 35-342 (Pl. V fig. 1 a,b): a part of the flank of a fish 117 mm long, in lateral view, with squamation and pectoral, pelvic and anterior dorsal fin-spines. LGMTI 35-350 (Pl. VI fig. 2): a specimen in lateral view, 67 mm long, with pectoral, pelvic and anterior dorsal fin- spines and squamation.

Occurrence. Uppermost part of the Severnaya Zemlya Formation, Lochkovian, Lower Devonian. Severnaya Zemlya Archipelago, October Revolution Island, the Pod'yomnaya River, outcrop 67, bed 12; the Matusevich River, outcrop 1, bed 21 and the Spokoinaya River, outcrop 41, bed 12.

Description. Body shape and proportions. Most of the individuals are exposed in lateral view and only a few are dorso-ventrally flattened. The fish reconstruction (Text-fig. 1), has been made on the basis of the eight most informative specimens. The length of the most adult individuals apparently reached 230-250 mm (Text-fig. 2). The body is slender and torpedoidal. Judging from well-preserved articulated jaw-bones available in the collection (specimens LGMTI 35-355, 35-360), the head was up to 60-65 mm long, which makes about 24 % of the body length. The two powerful and long dorsal fin-spines are arranged at the distance of 70 mm from one another. The body length from the front end of the head to the anterior dorsal fin-spine approximately equals the distance between the dorsal fin-spines. The paired pectoral fins are placed slightly in front of the anterior dorsal fin-spine, their greatest length being 56 mm. The anal fin-spine is arranged against the posterior dorsal fin-spine or a little behind it. The shorter and narrower paired pelvic fins are situated approximately halfway between the dorsal spines. In juveniles the fin-spines are of the same proportions. The collection contains some specimens of juveniles 27-42 mm long.

The jaws. The lower and upper jaw-bones consist of a single ossification. The palatoquadrate cartilage is not dismembered to the quadrate, metapterygoid or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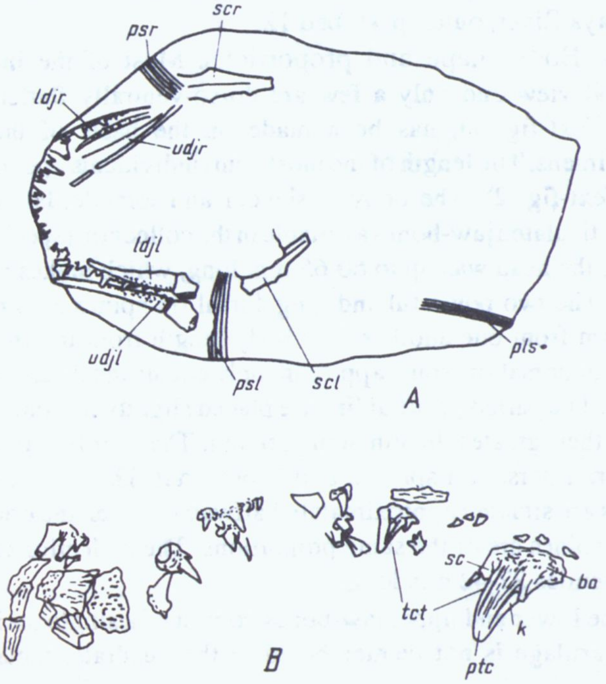
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autopalatinum. In the lateral view (Text-fig. 3A) it has the trapezoidal form. In the well preserved specimen LGMTI 35-358 the palatoquadrate cartilage is about 33 mm long and about 11 mm high. Its anterior part is widened and has a groove for circumorbital plates. Along the posterior edge there is a narrow extrapalatoquadrate crest. The articular process is distinctly expressed, entering the corresponding recess in the meckelian cartilage. The articular apparatus permitted the mouth to be widely opened for a powerful and effective bite. The meckelian cartilage consists of a single element, and in the lateral projection it makes up 2/3 of the palatoquadrate height.

Dentition. The lower and upper articulated jaws (specimens LGMTI 35-355, 35-358, 35-360) bear large sharp teeth. The lower jaw is slightly longer than the upper one, 33 and 29 mm, respectively (after LGMTI 35-358). The lateral gnathal bone ridge carrying the main lateral tooth row, has a more complicated quadrangular form in the transverse section. From the inner side, the mesial ridge proceeds to the lateral ridge (Text-fig. 3 B). It is slightly widened and is higher at the posterior part (where there are the smallest low teeth in the lateral tooth row), but narrows down and lowers in the anterior part. Between these two parallel ridges there is a narrow and deep groove. Both rami of the jaws bear up to nine principal cusps with small teeth between them. As one can see in the specimen LGMTI 35-360 (Text-fig. 6), three posterior teeth are the smallest, 0.75-1.2 mm in height. Behind them there is the part of the jaw without teeth and only with round low denticles. The following four teeth are the largest. The height of the teeth of the specimen LGMTI 35-360 is the greatest, amounting to 7 mm. In the anterior part of the jaw the teeth lower again. In the cross palatobasal section, the teeth of the main row have a slightly roundish-triangular or oval form. At this place they are heavily thickened and carry two or three longitudinal sharp keels (Text-fig. 5D, 6B). The teeth apices are thinner, conical or round in cross section. The teeth are bent mesiocaudally. Nearly all these principal teeth are threecuspidate (Text-fig. 6B). One small tooth adhears to the side of the large principal cusp. Only in rare cases these side cusps grow up to a half-height of the principal one. About five low wide-based conical monocuspidate small teeth may occur in every intercusp pit between the large threecuspidate teeth. On the large cusps there are longitudinal wavy striae. In the well- preserved individuals one can see that when the jaws are closed the large threecuspidate teeth lock perfectly into intervals with the small intercusps on the opposite jaw (Text-figs. 3A, 4A, 7A). At the anterior edge of the mandibular bone, as seen in the specimen

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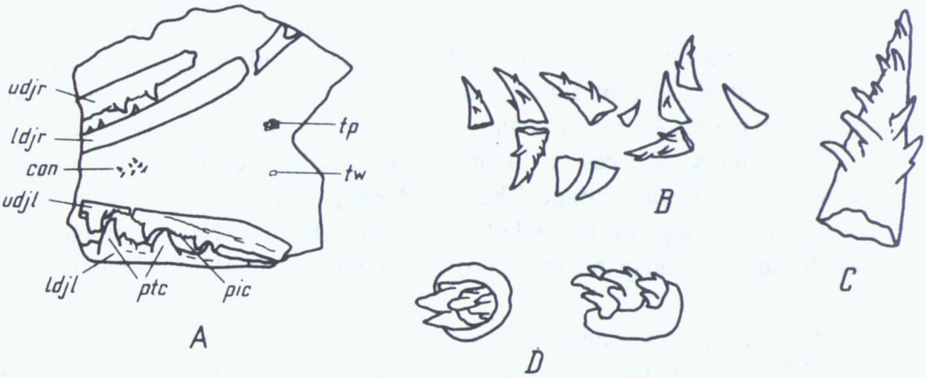
Text-fig. 5. A - parts of the lower jaw-bones with tooth-whorl in lateral view. Paratype, LGMTI 35-354 (Pl. III fig. 1a), x 2; B - tooth-whorl of the same specimen, x 8; C - denticles disposed on the side of the jaw-bone in the same specimen, x 50; D - part of the left lower dentigerous jaw-bone showing the shape of principal tooth-cusps on lateral ridge and denticles on mesial ridge. Specimen 35-351 (Pl. IV fig. 3), x 4.

Text-fig. 6. A - upper and lower dentigerous jaw-bones, paired pectoral fin-spines, paired scapulae and pelvic fin-spine. Holotype, LGMTI 35-360 (Pl. I fig. 1), x 1; B - threecuspidate teeth in anterior part of the lower jaw in holotype (Pl. I fig. 2), x 4.



Text-fig. 7. A - paired opposing jaw-bones with teeth of main tooth row and disposed between them cones, tessera-like ornamented plates and tooth-whorl. LGMTI 35-349, x 1.5; B - disposition of some tooth-like cones of dentition or branchial apparatus in the area between jaw-bones, x 12; C - one of the cones, x 45; D - small tooth-whorl consisting of threecuspidate teeth, top and side views, x 20.

LGMTI 35-354 (Text-fig. 5A,B), there is the tooth-whorl consisting of three bent threecuspidate teeth. Most of the individuals have well-preserved thin sharp separate palatine- teeth of 0.3-0.6 mm in height (Text-fig. 4C). The tooth-like denticles cover posterior 2/3 of the upper part and the sides of the mesial ridge slightly advancing onward (Text-fig. 5D). They have a round cross-basal section, blunt apices and streamy longitudinal ribs, and grow up to 1 mm in height.

Teeth histology. The bone tissue of the jaws is closely bounded and gradually turns into the osteodentine of the teeth. In the jaw tissue there are large vascular canals, some of which turn in their upper parts into the tooth-pulp canals. As shown in Text- fig. 9D, the separate vascular canals of the jaw form a capsule around themselves which differs in colour and structure from the rest of the tissue. Gross (1971) called it a "Denton", Ørvig (1973), following him, a denteon. The same tissue covers the tooth-pulp canals (Text-fig. 8E,G, 10D). In all the cases one can note a thin lamellarity of the osteodentine as well as orientation of the layer components around the vascular canal. The denteon layer becomes thinner in the direction of the tooth apex. In the jaw bone and the tooth basal layer there are numerous cavities of osteocytes that have also some orientation in the space

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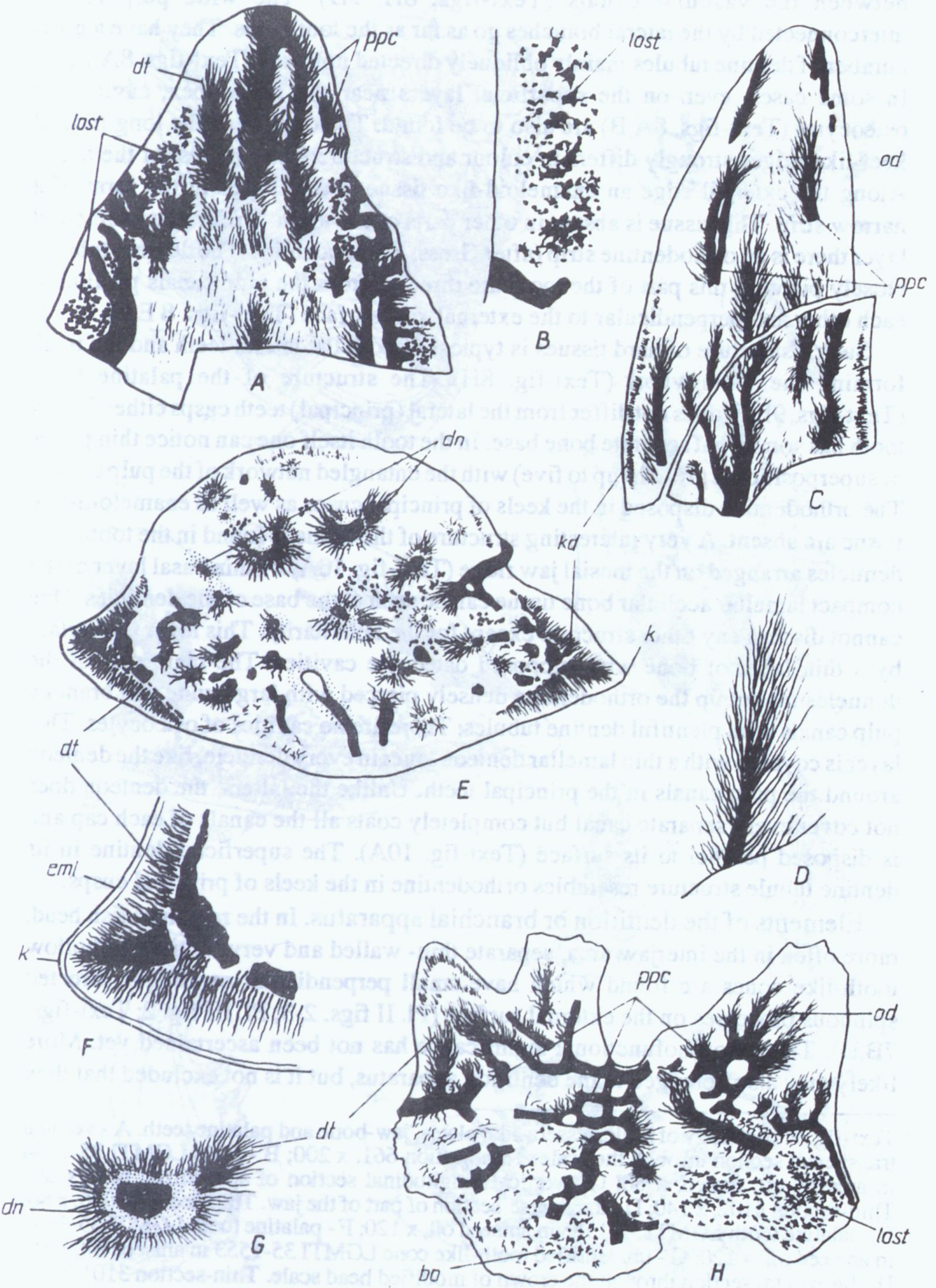
Text-fig. 8. Histology of teeth. A - vertical longitudinal section through the apex of the tooth. Thin-section 3097, x 80; B - part of the same section in higher magnification, x 200; C - vertical longitudinal section of tooth with sharp side-keels. Thin-section 3098, x 80; D - orthodentine of central part in the same section, x 200; E - transversal section through the basal part of the tooth with sharp side-keels. Thin-section 3095, x 56; F - structure of dentine of the keel in the left part of the same section, x 200; G - detail of pulp canal and denteon in the same section, x 300; H - vertical longitudinal section of part of the tooth-whorl. Thin-section 3103, x 56.

A-G - specimen LGMTI 35-351, the Matusevich River, outcrop 1, bed 21; H - specimen LGMTI 35-360, the Pod'yomnaya River, outcrop 67, bed 12.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between the vascular canals (Text-figs. 8H, 9D). The wide pulp canals interconnected by the lateral branches go as far as the tooth tops. They have a great number of dentine tubules mainly obliquely directed upwards (Text-figs. 8A,C,D). In some cases, even on the superficial layers near the tooth apex, cavities of osteocytes (Text-figs. 8A,B) are also to be found. The dentine of the longitudinal keel-like ridges strongly differs in colour and structure from the rest of the tooth. Along the external edge an enameloid-like tissue is developed in the form of a narrow strip. This tissue is absent in other parts of the tooth. Under that enameloid layer there is an orthodentine strip (after Gross, Kantendentin). The dentine tubules closely piercing this part of the tooth are directed from the pulp canals parallel to each other and perpendicular to the external keel surface (Text-figs. 8 E,F).

Such a structure of hard tissues is typical of both the lateral teeth and the teeth forming the tooth-whorl (Text-fig. 8H). The structure of the palatine teeth (Text-figs. 9E,F) does not differ from the lateral (principal) teeth cusps either. Every tooth has somewhat separate bone base. In the tooth itself one can notice thin plates of superpositional growth (up to five) with the entangled network of the pulp canals. The orthodentine disposed in the keels of principal cusps as well as enameloid-like tissue are absent. A very interesting structure of the tissue is found in the tooth-like denticles arranged on the mesial jaw ridge (Text-fig. 10A). A thin basal layer of the compact lamellar acellular bone tissue can be seen at the base of the denticles. One cannot discern any other structure except for the lamellarity. This layer is overlain by a thin layer of bone with supposed osteocyte cavities. The main part of the denticles makes up the orthodentine densely pierced with large wide and branchy pulp canals with plentiful dentine tubules. There are no cavities of osteocytes. This layer is covered with a thin lamellar denteon layer in every denticle, like the denteon around the pulp canals in the principal teeth. Unlike the latters, the denteon does not cover every separate canal but completely coats all the canals of each cap and is disposed parallel to its surface (Text-fig. 10A). The superficial dentine in its dentine tubule structure resembles orthodentine in the keels of principal cusps.

Elements of the dentition or branchial apparatus. In the region of fish head, more often in the interjaw area, separate thin- walled and very fragile and hollow tooth-like cones are found which have small perpendicular or oblique-directed spinuous processes on the external surface (Pl. II figs. 2-3; Pl. III fig. 2; Text-figs. 7B,D). Their morphofunctional significance has not been ascertained yet. More likely they also belonged to the dentition apparatus, but it is not excluded that they

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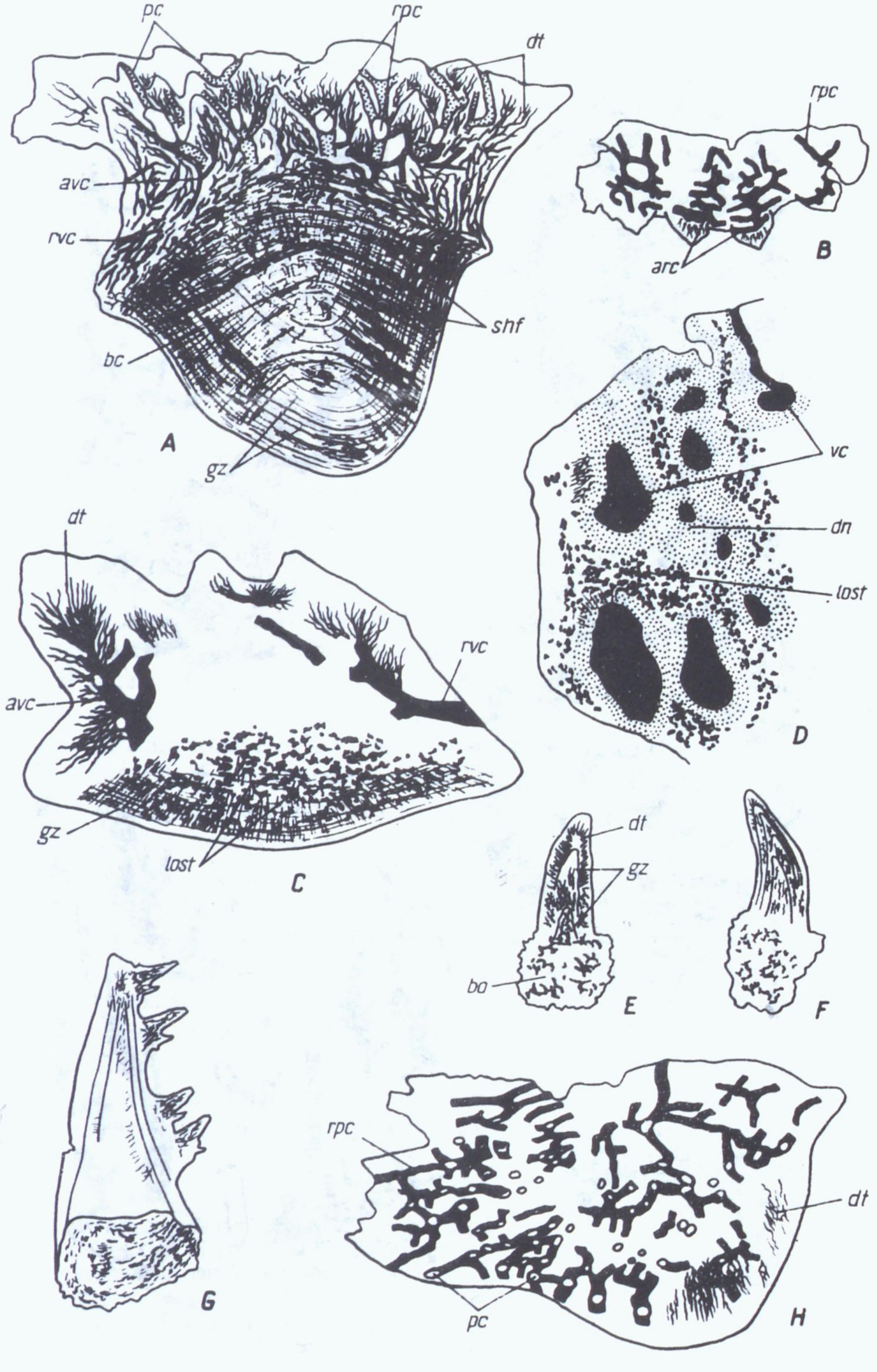
Text-fig. 9. Histology of scale, tessera-like plates, jaw-bone and palatine teeth. A - vertical transversal section through the scale. Thin-section 661, x 200; B - scale LGMTI 35-1554 in aniseed oil, crown, x 80; C - vertical longitudinal section of specialized head scale. Thin-section 3102, x 140; D - transverse section of part of the jaw. Thin-section 3096, x 80; E - palatine tooth LGMTI 35-1555 in aniseed oil, x 120; F - palatine tooth LGMTI 35-1556 in aniseed oil, x 120; G - unidentified tooth-like cone LGMTI 35-1553 in aniseed oil, x 80; H - horizontal section through the crown of modified head scale. Thin-section 3101, x 56. A - specimen LGMTI 35-367, B, E, F and G - specimen LGMTI 35-340, C and H - specimen LGMTI 35-360. All the specimens except D from the Pod'yomnaya River, outcrop 67, bed 12; D - specimen LGMTI 35- 351, the Matusevich River, outcrop 1, bed 21.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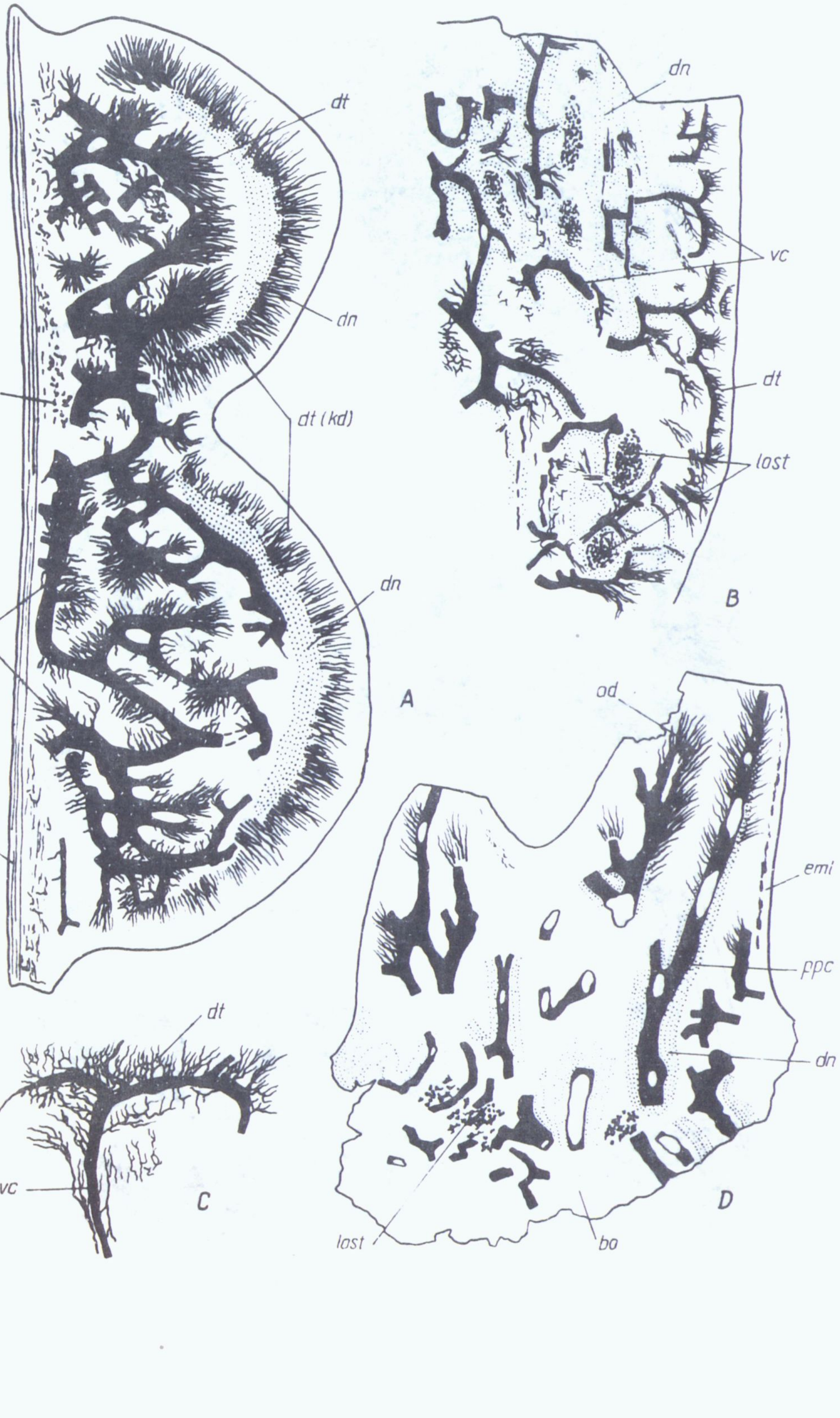
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may be assigned to the branchial one. The study of the histology of cone structure (Text-fig. 9G) did not solve the problem.

Shoulder-girdle. The endoskeletal shoulder-girdle consists of paired scapula. They both (the left and the right one) are straight and high, and, as shown on the specimen LGMTI 35-360 (Text-fig. 6A), are of 26 mm in height. Their lower (basal) part in projection is triangular, the upper part being semicircular. The basal 1/3 part is widened to 9 mm, while the upper part is 4- 5 mm in width.

Fin-spines. All the fin-spines have the same structure, differing only in size. They are slightly bent caudally. The central interior cavity is elongate oval in projection and nearly reaches the top. The approximate size of fin-spines, depending on the individual's length, may be estimated by their preserved fragments, the length of which is shown in Text-fig. 1. The powerful pectoral and anterior dorsal fin-spines might have been of 54-56 mm in length. The collection contains their well- preserved parts of 34 and 31 mm in length, respectively. The anal and posterior dorsal spines are approximately of the same dimensions: those of a very large individual might have reached 35-40 mm. The pelvic fin-spines are the smallest — about 30 mm in length. The general proportions between the separate parts of the spines may slightly change with growth. Thus adult individuals have an enlarged fin-spine width, a slightly greater lateral flatness and increasing number of the longitudinal ribs. They have always a clearly isolated thickened proximal rib separated from the rest of the ribs by a deep groove. The following four or five ribs are approximately of the same dimensions, stretching out along the whole spine. Towards the proximal edge, the rib widens slightly. On the distal half of the fin-spine there are about five low, narrow and sharp ribs. Between the distal and proximal halves there is sometimes a widened and gently sloping pinch. In juvenile individuals, the rib number decreases both in the proximal and the distal parts, so morphological differences between them are less noticeable.

Histology of the fin-spines. The differences become visible in the tissue structure of both the younger proximal and the older distal spine parts. The proximal part in fact does not differ from the principal teeth structure. Here there is always a big longitudinal central cavity (pulp) surrounded by a heavy layer of a thin lamellar bone and osteodentine (Text-fig. 11B). Large vascular canals proceed from the cavity brims including intermediate branches and processes. Most of such canals run in two directions — perpendicular to the external spine-wall and parallel to the brims of the cavities. Only the separate parts of this juvenile bone tissue have osteocytes (Text-fig. 10B). Then follows a weak layer of a similar bone in which

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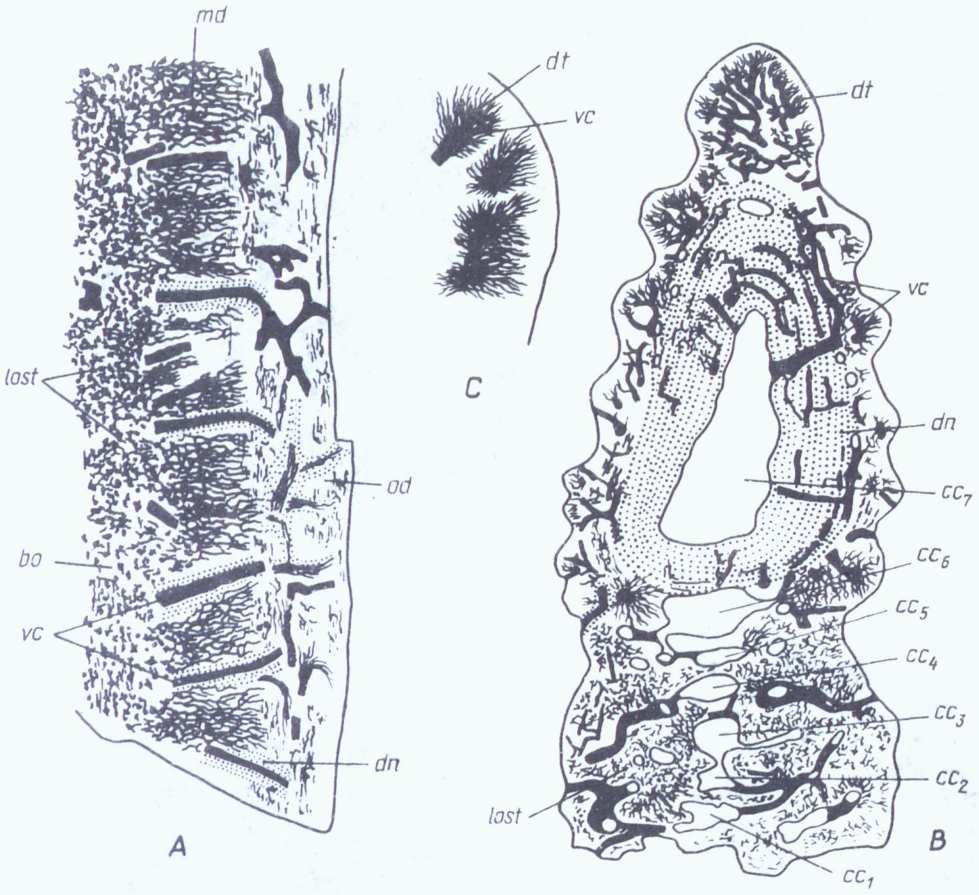
Text-fig. 10. Histology of teeth, denticles and fin-spine. A - vertical longitudinal section through two articulated denticles from mesial gnathal ridge. Thin-section 3100, x 140; B - longitudinal section of proximal part of fin-spine. Thin-section 3105, x 80; C - dentine canals in superficial part of fin-spine, the same section in higher magnification, x 200; D - vertical longitudinal section of two articulated teeth cusps. Thin-section 3094, x 56.
A - specimen LGMTI 35-349, B and C - specimen LGMTI 35-360, the Pod'yomnaya River, outcrop 67, bed 12. D - specimen LGMTI 35-351, the Matusevich River, outcrop 1, bed 21.

one can note an increase in the number of vascular canals and a decrease in their sizes. This layer gradually turns into a superficial mesodentine- like layer forming the ribbed spine part. The dentine tubules of the superficial layer are mainly perpendicular to the fin-spine surface and tissue structure resembles the orthodentine of the tooth keels. In the distal part there are some overgrowing cavities which have different forms and reflect different stages of the growing of the spine and its age (Text-fig. 11B). The tissue composing this fin-spine part is distinctly divided into three parts. The interior (peripulpar) layer of the bone includes numerous inoriented large osteocyte cavities with rare narrow and twisting processes (Text-fig. 11A). Here the large vascular canals are widely spaced and considerably reduced. The next layer of the bone-tissue is pierced with large vascular canals directed mainly to the external spine surface. The canals contain denteon as a capsule. The space between the canals is filled with the dense network of interweaved twisting vascular canals containing lacunae. This tissue is similar to a mesodentine of acanthodian scales. Between both layers one can note a gradual transition. In the basal part of the second layer there are also osteocyte cavities. The superficial dentine layer contains only widely- spaced vascular canals. There are no interweaved canals between them. The longitudinal fibres here are better expressed, resembling Sharpey's fibres in scales.

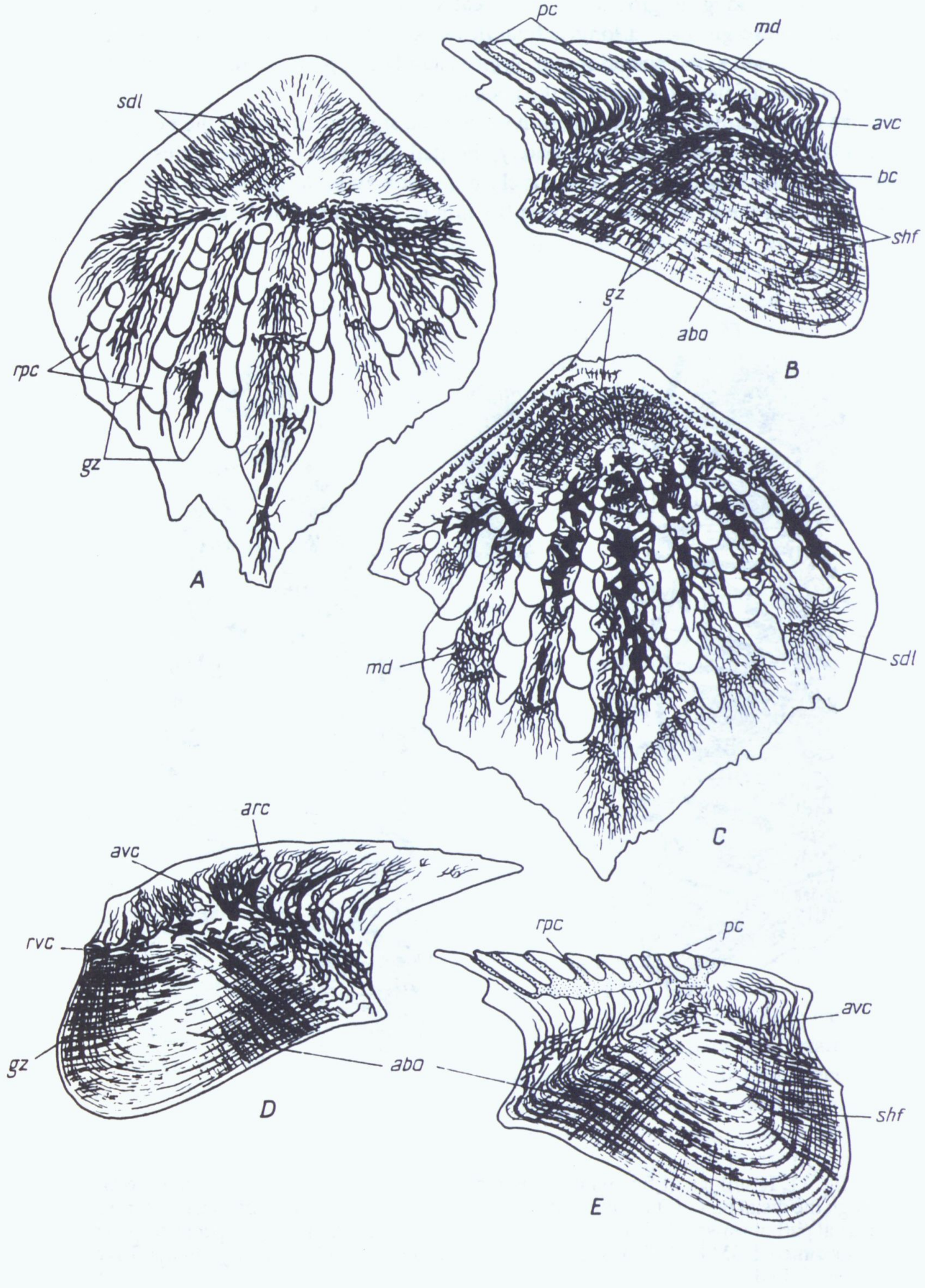
Squamation. The body of the fish is covered all over with slanting rows of closely-spaced small scales. A detailed study of their morphological features has shown that the variability of scales located on different parts of the body is not remarkable. The head region is most clearly distinguished, whereas the rest of the body parts (their approximate boundaries are shown in Text-fig. 2) have, in principle, no differences in squamation. Here the scales just slightly vary both in size and in configuration. The same may be said about the squamation of the juvenile individuals.

The head of the fish (I area) is covered with mutated scales of various sizes and tessera-like plates. The size of the latter has a wide range of variation from 0.3-0.4 mm to 4.2 mm (Pl. IX figs. 2-6), in one individual. As a rule, their length is significantly less than the width, the neck is low and the base varies from being slightly prominent to flat or concave. The crown of the plates is very variable. Usually there are some lateral areals with a longitudinal slope-ridged ornament (Pl. IX figs. 2-5). The areals may be either divided from each other by more considerable grooves, or accreted with each other without noticeable boundaries. Pore-canals are located in grooves between the areals as well in the grooves between certain ridges of the crown. We met less frequently with plates that have a distinguished large, nearly unornamented or even central areal and sprouts, prominences and "rosettes" of different shape located along the edges (Pl. VIII fig. 5). There is one more variety of plates that have a structure approximating normal scales (see Pl. IV fig. 6). They have an isolated proximal areal that is a little higher than the rest of the crown and is subdivided into fine separate ridges with grooves. The rest of the laterodistal part is tightly accreted. Concentric slope grooves stretching along the distal edge of the crown and marking its growth, can be clearly seen. The pore canals are usually located in these grooves in longitudinal or radial rows that run from the anterior edge of the scale to the posterior one. A great number of pore canals open onto the lower surface of the crown and in the neck as well.

The second area of the squamation occupies a significant part of the body and extends from the head to, approximately, the anal fin-spine. Here the scales have a flat, diamond-shaped crown, a relatively high neck and a large, protruding base. The length of their crown varies from 0.7 mm to 1.35 mm. The largest scales are



Text-fig. 11. Histology of fin-spine of adult individual. A - vertical longitudinal section through the distal part of fin- spine. Thin-section 3105, x 80; B - transverse section through the basal part of fin-spine. Thin-section 3106, x 56; C - detail of the same specimen, x 300. A - specimen LGMTI 35-360 and B - specimen LGMTI 35-371, Pod'yomnaya River, outcrop 67, bed 12.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usually located in the anterodorsal division. There up to eight concentric grooves on the crown that stretch parallel to its posterior edge and show the boundaries of the growth plates. Pore-canals open up in straight lines in these grooves. There are usually four such lines (Pl. VI fig. 1 b; Pl. X figs. 2-5). The third area of squamation is behind the anal fin-spine. The scales do not differ in principle from the ones described above but are smaller in size and their crown is more narrow and elongated (Pl. X figs. 6-7 and 9). The length of the crown is 0.5-0.8 mm.

Besides these three basic areas, there may be noted some small areas at the fin-spines where the scales are somewhat different. At the dorsal spines (fourth area) the scales are usually larger and more massive, and they have a thicker crown (Pl. X figs. 1- 2). An even border without pore-canals runs along the anterior edge of the crown of such scales. Concentric line grooves (growth plates) are to be noticed, as a rule, only in the distal half and sometimes only at the distal end of the crown. The smallest (0.5- 0.6 mm), longitudinally extended, often slightly asymmetrical scales (Pl. X fig. 8) are located in a limited area at the anal fin-spine.

Scale histology. There are up to ten growth lamellae in the crown. The growth is of the areal type, taking place in the laterodistal areals by adding every next lamella from below and from the sides. So the upper part of the lamellae is not overlapped. A complex system of large pore canals is developed in the crown of the scale, consisting of concentric arcade and linearly extended longitudinal, radial and superficial canals (Text-fig. 12). Narrow pore-canals run upwards and open outside. As the scale is growing, a new large arcade canal is formed in every new lamella (in the basal layer). The radial pore-canal joints precisely to the canal of the previous lamella, thus adding a little to the size (Text-figs. 12A,C). Mesodentine tissue is densely penetrated by radial and ascending vascular canals containing a lot of interwoven tubules (Text-figs. 12B,D). Radial vascular canals are very complex and multibranched above the base of the scales. Some large branches are oriented down, towards the base (Text.-fig. 12B). Wide and continuous ascending canals are formed in every growth plate. They are joined by multiple lateral branches and tubules. There are no osteocyte cavities or lacunae. The base of the scale is composed of thin lamellae of acellular bone; it contains sinuous short canals and long Sharpey's fibres (Text-figs. 12D,E).

Head tesseral-like plates and mutated scales have a slightly different tissue structure. There is often hardly enough place for the development of vascular canals here because of their large size and a great number of pore-canals (Text-figs. 9B,H). In cases when they are found (Text-fig. 9C), an extraordinary width of radial and ascending branches as well as panicle-like location of their tubules is noted. Their base is composed of the bone tissue with cavities of large polygonal osteocytes (Text- fig. 9C).

Text-fig. 12. Histology of body scales. A and C - horizontal sections of crown of scales. Thin-sections 662 and 660, x 200; B, D and E - vertical longitudinal sections of scales. Thin-sections 659, 663 and 664, x 200.
All the scales from specimen LGMTI 35-367, the Pod'yomnaya River, outcrop 67, bed 12.

Comparison. *Poracanthodes menneri* sp.n. differs from *P. punctatus* Brotzen in lacking parallel ridges and grooves on the anterior part of the crown, concentric grooves on the posterior one, the areal type of growth (superpositional in *P. punctatus*), and more multibranched ascending and superficial vascular canals. From *P. porosus* Brotzen it differs in a constant number of radial pore-canals, the presence of well- developed arcade pore-canals, and more complex radial vascular canals placed in the neck of the scales. From *P. gujingensis* Wang the species differs in the absence of ridges on the anterior part of the crown and a higher neck. In *P. gujingensis* the pore-canals on the surface of scales are the largest, and the ridges on the posterior part are the longest and highest; the crown of the scales in this species is composed of dentine with less complex vascular canals.

Concluding remarks. Summing up, the following aspects should be emphasized:

1. The finds of articulated specimens of *Poracanthodes menneri* sp.n. should put an end to the confusion of ischnacanthiform system and provide a possibility to avoid joining the genera *Gomphonchus* and *Poracanthodes*. Most of researchers who studied the isolated scale material did not recognize *Poraconthodes* as an independent genus. The scales of *Poracanthodes* were regarded as modified lateral line scales of *Gomphonchus*. This opinion was expressed e.g. by Denison (1979). In this connection it may be necessary to emphasize that we have not found specialized lateral line scales in *Poracanthodes menneri* sp.n.
2. The specific structure (both the morphological and histological aspects) of all skeletal elements of *Poracanthodes menneri* sp.n. raises the problem of a higher rank of this genus in the order Ischnacanthida. It seems to be necessary to establish the family *Poracanthodidae*, including into it all the representatives of the ischnacanthiform acanthodians, in particular those having a complex system of pore-canals in their scales.
3. When studying the isolated scale material, one should approach with great care the problems of possible topographical variability of the scales as well as composing the so-called morphological series. The whole body of *Poracanthodes menneri* sp.n., excluding the head region, is covered with insignificantly variable scales.

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For other references see Denison, 1979.

Abbreviations used in text-figures

abo - acellular bone, ADS, ads - anterior dorsal fin-spine; AS, as - anal fin-spine, avc - ascending vascular canal, arc - arcade-pore canal, bas - base of scale, bc - canals in the base of scale, bo - bone, cc - central cavity of fin-spine, cc_{1-7} - central cavities of growth zones in fin-spines, con - tooth-like cone of dentition or branchial apparatus, dn - denteon, dt - dentine tubule, dtc - denticles (odontodes) on the mesial ridge of dentigerous jaw-bone, dt(kd) - dentine tubules of orthodentine in keels of teeth, eml - enameloid, expc - extrapalatoquadrate crest, gz - growth zones; JGB, jgb - jaw (gnathal) bone, k - keel of tooth, kd - orthodentine in keels, latr - lateral ridge of dentigerous jaw-bone, lbo - lamellar bone, ldj - lower dentigerous jaw-bone, ldjl - left lower dentigerous jaw-bone, ldjr - right lower dentigerous jaw-bone, lost - lacunae of osteocytes, md - mesodentine, mesr - mesial ridge of dentigerous jaw-bone, mk - meckelian cartilage, od - orthodentine, pc - pore- canal; PDS, pds - posterior dorsal fin-spine, pic - intercusp pit in main tooth row; PLS, pls - pelvic fin-spine, ppc - pulp canal, prart - articular process, ps - pectoral fin-spine, psl - left pectoral fin-spine, psr - right pectoral fin-spine, ptc - principal cusp of main tooth row, pq - palatoquadrate, rpc - radial pore-canal, rvc - radial vascular canal, sc - side cusp of threecuspidate tooth, scl - left scapula, scr - right scapula, sdl - superficial dentine layer, shf - tubules of Sharpey's fibres, tct - threecuspidate tooth, tp - tessera-like plates covering the head, tw - tooth-whorl, ttw - teeth of the tooth-whorl, vc - vascular canal, udjl - left upper dentigerous jaw- bone, udjr - right upper dentigerous jaw-bone.

Plate I
Poracanthodes menneri sp.n.
Fig. 1. Dorso-ventrally compressed specimen, holotype, LGMTI 35- 360. Upper and lower dentigerous jaw-bones, paired pectoral and pelvic fin-spines, shoulder-girdle, and squamation are preserved x1. The Pod'yomnaya River, outcrop 67, bed 12; Lower Devonian, Lochkovian, Severnaya Zemlya Formation.
Fig. 2. Threecuspidate teeth, anterior part of the lower jaw-bone in the same specimen (LGMTI 35-360). x 4.

Plate II
Poracanthodes menneri sp.n.
Fig. 1. Left palatoquadrate and meckelian cartilage, and articulated lower and upper jaw-bones with teeth in lateral view. LGMTI 35-358. x 2.
Fig. 2, 3. Unidentified tooth-like cones of dentition or branchial apparatus. LGMTI 35-1462 and 35-1459, respectively. x 40.
Fig. 4. Disarticulated fish in lateral view. Palatoquadrate and meckelian cartilage, fin-spines and squamation are visible. LGMTI 35-361. x 1.
All the specimens from the Pod'yomnaya River, outcrop 67, bed 12.

Plate III
Poracanthodes menneri sp.n.
Fig. 1a. Part of the lower dentigerous jaw-bone with the tooth- whorl. LGMTI 35-354. x 2; 1b. Tooth-whorl of the same specimen. x 8. the Spokoinaya River, outcrop 41, bed 12.
Fig. 2. Tooth-like cone of dentition or branchial apparatus. LGMTI 35-1460. x 40.
Fig. 3. Right pair of opposing dentigerous jaw-bones with teeth, in lateral view. LGMTI 35-349. x 2. 35-1460 and 35-349 from the Pod'yomnaya River, outcrop 67, bed 12.
Fig. 4. Juvenile fish in lateral view showing dorsal and anal fin-spines and squamation. LGMTI 35-365. x 2. The Matusevich River, outcrop 1, bed 21.

Plate IV
Poracanthodes menneri sp.n.
Fig. 1. Head of the fish in lateral view; left lower and upper dentigerous jaw-bones with teeth and tessera-like plates covering the head. LGMTI 35-355. x 3. The Pod'yomnaya River, outcrop 67, bed 12.
Fig. 2, 3. Disarticulated dentigerous jaw-bones with teeth in LGMTI 35-351. x 4. The Matusevich River, outcrop 1, bed 21.

Plate V
Poracanthodes menneri sp.n.
Fig. 1a. Part of the flank of fish. Squamation, pectoral, pelvic and anterior dorsal fin-spines. LGMTI 35-342. x 1. 1b. Squamation area near the dorsal fin-spine in the same specimen. Bases of scales visible. x 10. The Spokoinaya River, outcrop 41, bed 12.
Fig. 2. Disarticulated fin-spines, parts of jaw-bones and squamation. LGMTI 35-340. x 1. The Pod'yomnaya River, outcrop 67, bed 12.

Plate VI
Poracanthodes menneri sp.n.
Fig. 1a, b. Squamation of the second area in LGMTI 35-343. a - x 2, b - x 20. The Matusevich River, outcrop 1, bed 21.
Fig. 2. Part of the flank of fish showing squamation, anterior dorsal, pectoral and pelvic fin-spines. LGMTI 35-350. x 1. The Pod'yomnaya River, outcrop 67, bed 12.

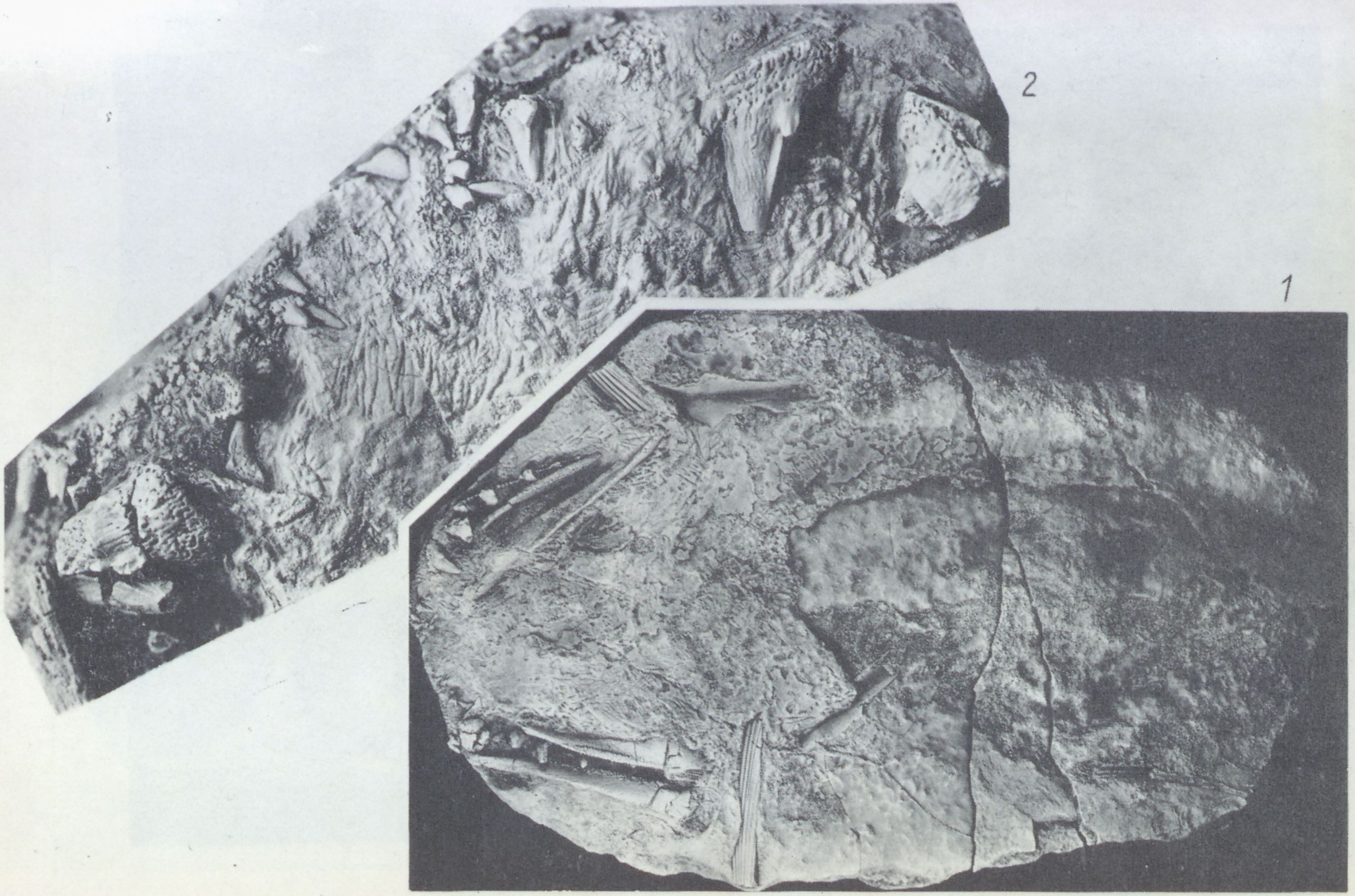

Plate I

Plate II

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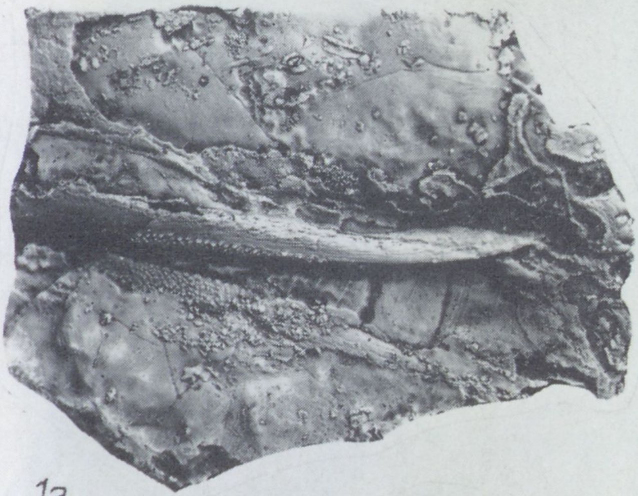
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Plate IV

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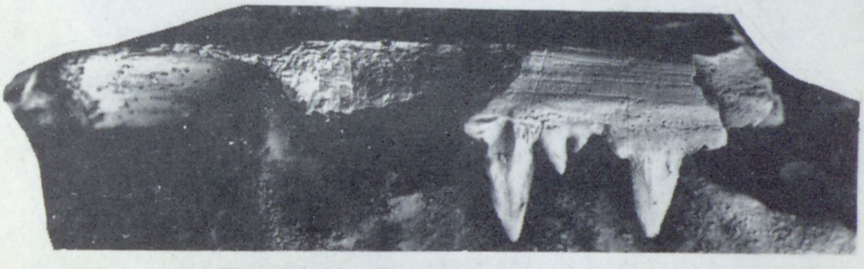

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Plate V

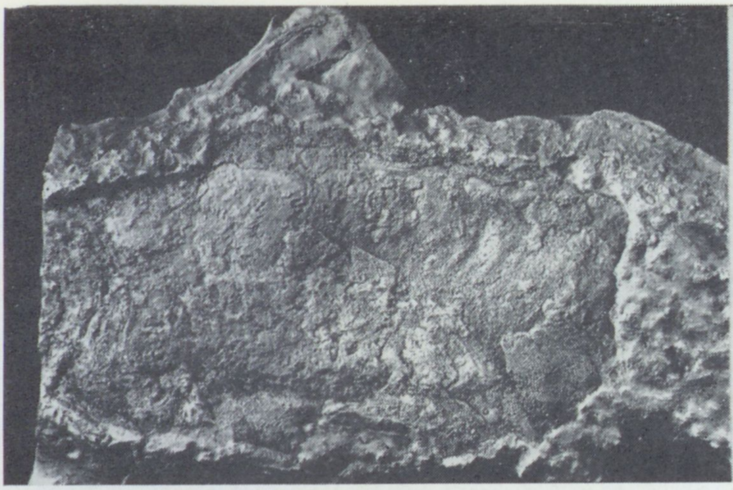
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Plate VI


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Plate VII


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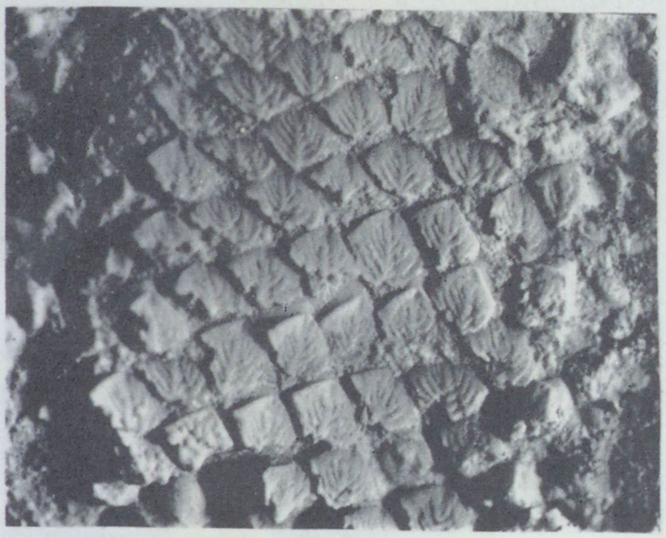
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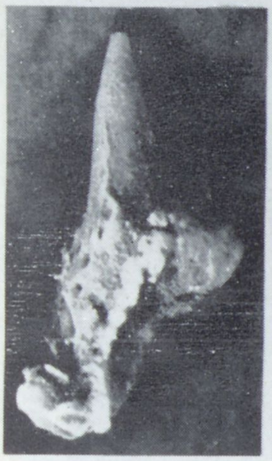
Plate VIII



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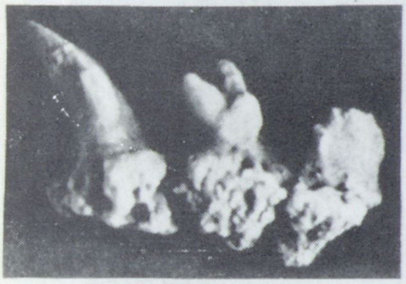

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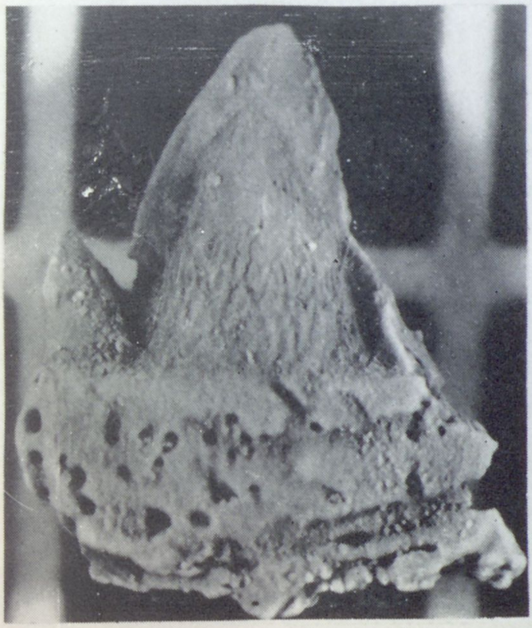

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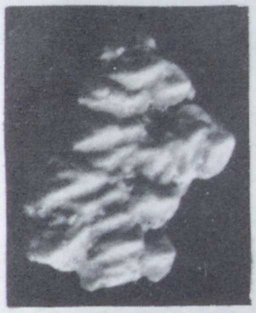

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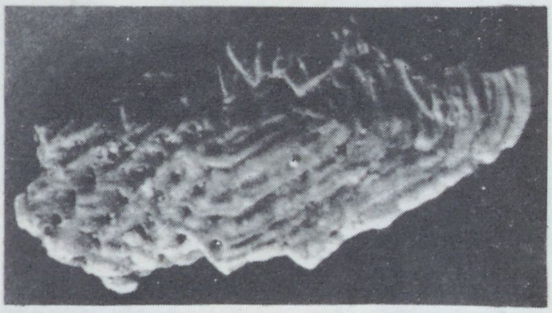

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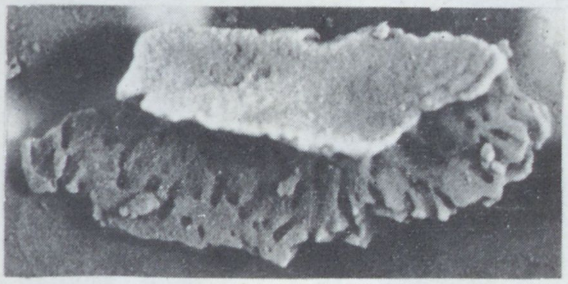

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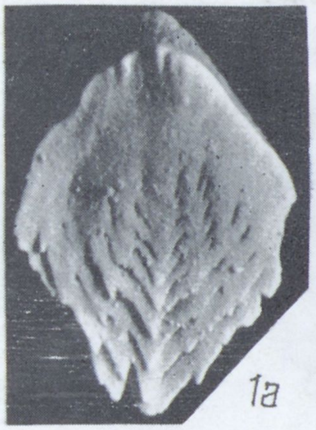
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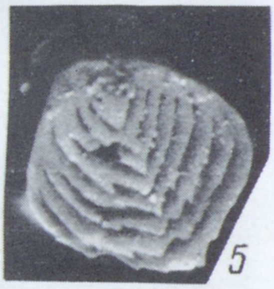
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8b


9b

Plate VII
Poracanthodes menneri sp.n.
Fig. 1a. The second area of squamation from the middle of the body with dorsal, pectoral and pelvic fin-spines. LGMTI 35-341. x 1. 1b. Scales in the same specimen, crowns exposed. x 20. The Pod'yomnaya River, outcrop 67, bed 12.
Fig. 2. Some flank scales, crowns of the second area of squamation. LGMTI 35-1457. x 30.
Fig. 3. Crown of an elongated scale of the third area of squamation. LGMTI 35-1471. x 40.
35-1457 and 35-1471 from The Pod'yomnaya River, outcrop 67, bed 12.

Plate VIII
Poracanthodes menneri sp.n.
Fig. 1. Monocuspidate tooth from the tooth-whorl, lateral view. LGMTI 35-1463. x 40.
Fig. 2. Palatine teeth, lateral view. LGMTI 35-1464. x 40.
Fig. 3. Threecuspidate tooth, lateral view. LGMTI 35-1468. x 15.
Fig. 4. Dorsal fin-spine and squamation. LGMTI 35-362. x 2.
Fig. 5. Tessera-like plate (crown) from the head area . LGMTI 35- 1461. x 40.
Specimens in Figs. 1-3 and 5 from the Pod'yomnaya River, outcrop 67, bed 12; in Fig. 4 from the Matusevich River, outcrop 1, bed 21.

Plate IX
Poracanthodes menneri sp.n.
Fig. 1a, b. Part of the mesial ridge of gnathal bone with denticles: a - top, b - side. LGMTI 35-1469. x 15.
Fig. 2 - 6. Tessera-like plates from the head area. 2 - LGMTI 35- 1466, 3 - LGMTI 35-1434, 4 - LGMTI 35-1435, 5 - LGMTI 35-1450. All figs. - x 40. 6 - LGMTI 35-1470, a - crown, b - base. x 15. All the specimens from the Pod'yomnaya River, outcrop 67, bed 12.

Plate X
Poracanthodes menneri sp.n.
Fig. 1 - 9. Scales. 1 - LGMTI 35-1458, a - crown, b - base, 2 - LGMTI 35-1465, crown, 3 - LGMTI 35-1454, crown, 4 - LGMTI 35- 1453, a - crown, b - lateral view, 5 - LGMTI 35-1455, crown, 6 - LGMTI 35-1448, crown, 7 - LGMTI 35-1451, a - crown, b - lateral view, 8 - LGMTI 35-1449, a - crown, b - lateral view, 9 - LGMTI 35-1456, a - crown, b - lateral view. x 40. All specimens from the Pod'yomnaya River, outcrop 67, bed 12.

Some data on the ontogeny of Devonian dipnoans

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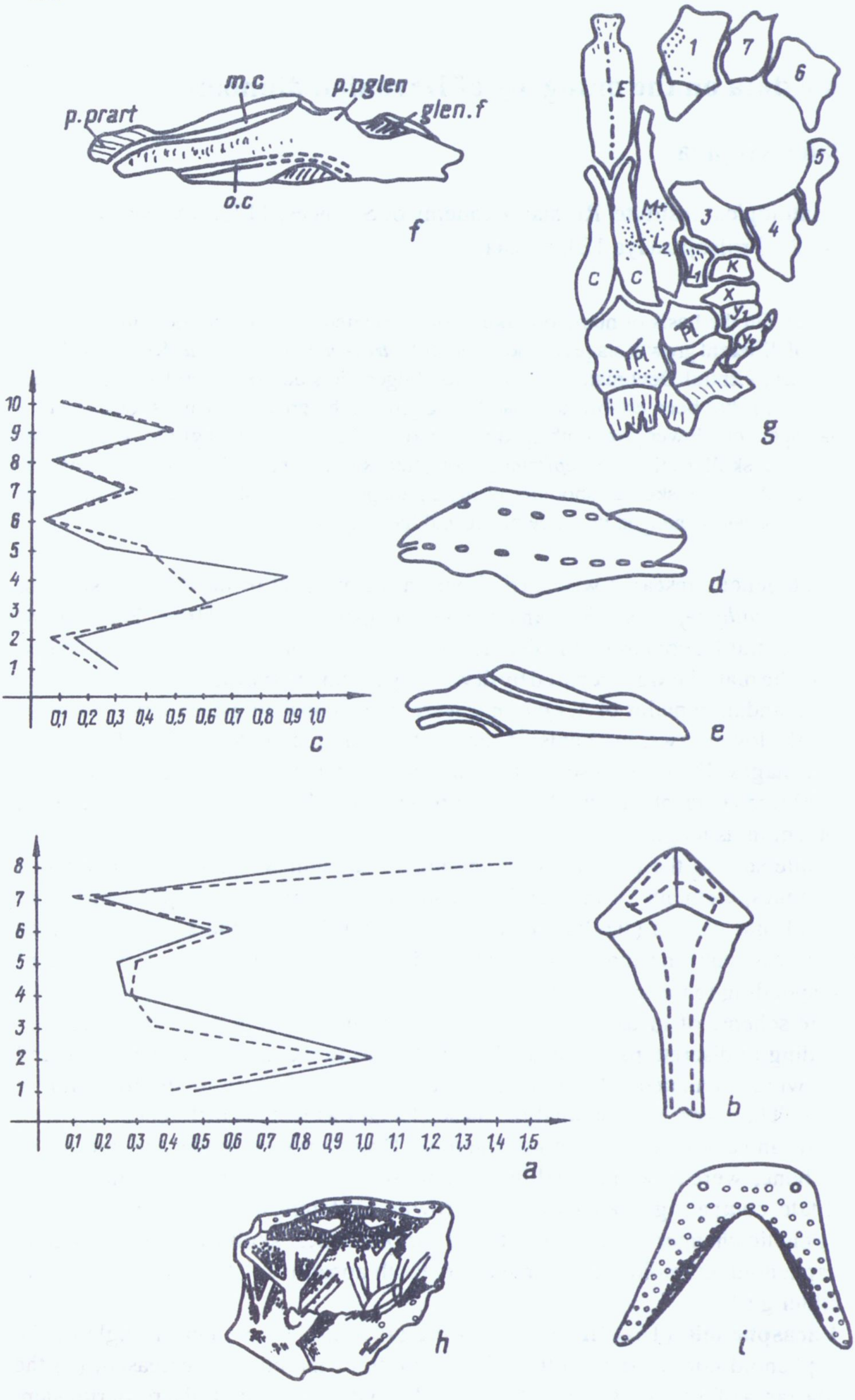
Abstract. On the basis of numerous skull bones, elements of the dentition and shoulder girdles of different growth stages of the dipnoan *Andreyevichthys epitomus* Krupina (Upper Famennian, Central Devonian Field) the morphogenetic study of several structures was carried out. It has been established that during growth the greatest changes took place in the parasphenoid, lower jaw, tooth apparatus, and exoskeletal shoulder girdle. The anterior part of the skull roof of *A. epitomus* elongated significantly, the juvenile dentition disappeared, the exoskeletal shoulder girdle developed considerably. Reaching the adult stage, *A. epitomus* changed its mode of life and feeding mechanism.

Our ontogenetic research was carried out on the material of the dipnoan species, *Andreyevichthys epitomus* Krupina, from the Upper Devonian (Upper Famennian) of the Central Devonian Field, Tula Region, locality Andreyevka-2 (see Krupina, 1987). The material was prepared by dissolving the bone-bearing rock in 10% acetic acid. Abundant remains of *A. epitomus* were found consisting of separate bones of the skull, lower jaws, elements of the dentition and shoulder girdle of different growth stages. The sizes of separate bones vary from 0.5 mm (tooth plates) to more than 70 mm (parasphenoids). So, it can be concluded that an adult fish exceeded 50-60 cm in its length.

While sorting the material after chemical treatment we picked out numerous skull bones, elements of the dentition and shoulder girdle. The specimens were grouped into growth (size) series beginning with those of the earliest juveniles (bones less than one mm in size) and ending with the large ones (several cm) corresponding to the adult stage.

The scheme of measurements was worked out for every bone and structure according to discrete parameters. Tables of measurements were constructed, and ratios were calculated. These ratios characterize the changes in structure during growth. They were used to analyze these changes as well as differences between juvenile and adult stages for some structures. Drawings were made, and outlines of adult bones were superimposed in the same scale as the juvenile ones in order to facilitate comparing changes during growth. Different degrees of accuracy of ontogenetic changes were interpreted in various bones: skull roof, orbital region, parasphenoid, ethmoid region, mandible, tooth apparatus, lateral line canals, and shoulder girdle.

Parasphenoid (Text-fig. 1a,b). During growth, (1) the anterior angle of the parasphenoid corpus and (2) the relative width of the corpus decreased; (3) the overlap area of the pterygoids on the parasphenoid increased; (4) the posterior stem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of the parasphenoid became relatively longer in comparison to the corpus length. In adults the length of the stem was almost twice the length of the parasphenoid corpus.

Mandible (Text-fig. 1c-f). During ontogeny, (1) the mandibular ramus and (2) the prearticular process became relatively longer; (3) the height of the ramus, and (4) the length of the oral canal decreased in relation to the length of the ramus; (5) the size of the preglenoid process (especially its height) and (6) the length of the mandibular canal slightly increased. Both the part of the ramus anterior to the anterior opening of the mandibular canal and the preglenoid process account for the lengthening of the mandibular ramus. This lengthening of the ramus took place because of the growth of the anterior part situated in front of the anterior opening of the mandibular canal, and it occurred due to the enlargement of the preglenoid process. The preglenoid process was not well developed in the juveniles: the glenoid fossa was absent.

Skull roof (Text-fig. 1g). During ontogeny the anterior and middle parts of the skull roof, i.e. bones C,E, and M+L_2 (according to the nomenclature by Westoll, 1949) elongated considerably. This is additional evidence of the total, relative elongation of the anterior part of the skull. The remaining bones of the skull roof grew more or less uniformly.

Circumorbital bones (Text-fig. 1g). All the bones of this series have two common features: (1) the margin of the bones forming the orbit became smaller in comparison to the juvenile stage; (2) there was a change of ratio between width and length of all the bones with the exception of bone 6. The circumorbitals 1, 3-5 and 7 grew longer in the direction opposite to the orbit.

Shoulder girdle (Text-fig. 2). The shoulder girdle changed considerably during the growth of Devonian dipnoans. In juveniles it was more poorly developed than in adults.

Supracleithrum (Text-fig. 2d-f; Plate, b). In juveniles, the contact zone between the supracleithrum and the anocleithrum was not developed. However, the contact area between the supracleithrum and bone Z was very small.

Anocleithrum (Text-fig. 2b,c; Plate, a,c). The extension and total area of the branchial lamina as well as the thickness of the ascending process of the anocleithrum became larger while growing. In the juveniles this bone seems to have had a narrow undeveloped branchial lamina and a short but relatively broad ascending process. The crest c_2 is unlikely to have been developed. The bone itself appears to have been relatively much shorter as compared to that of the definitive

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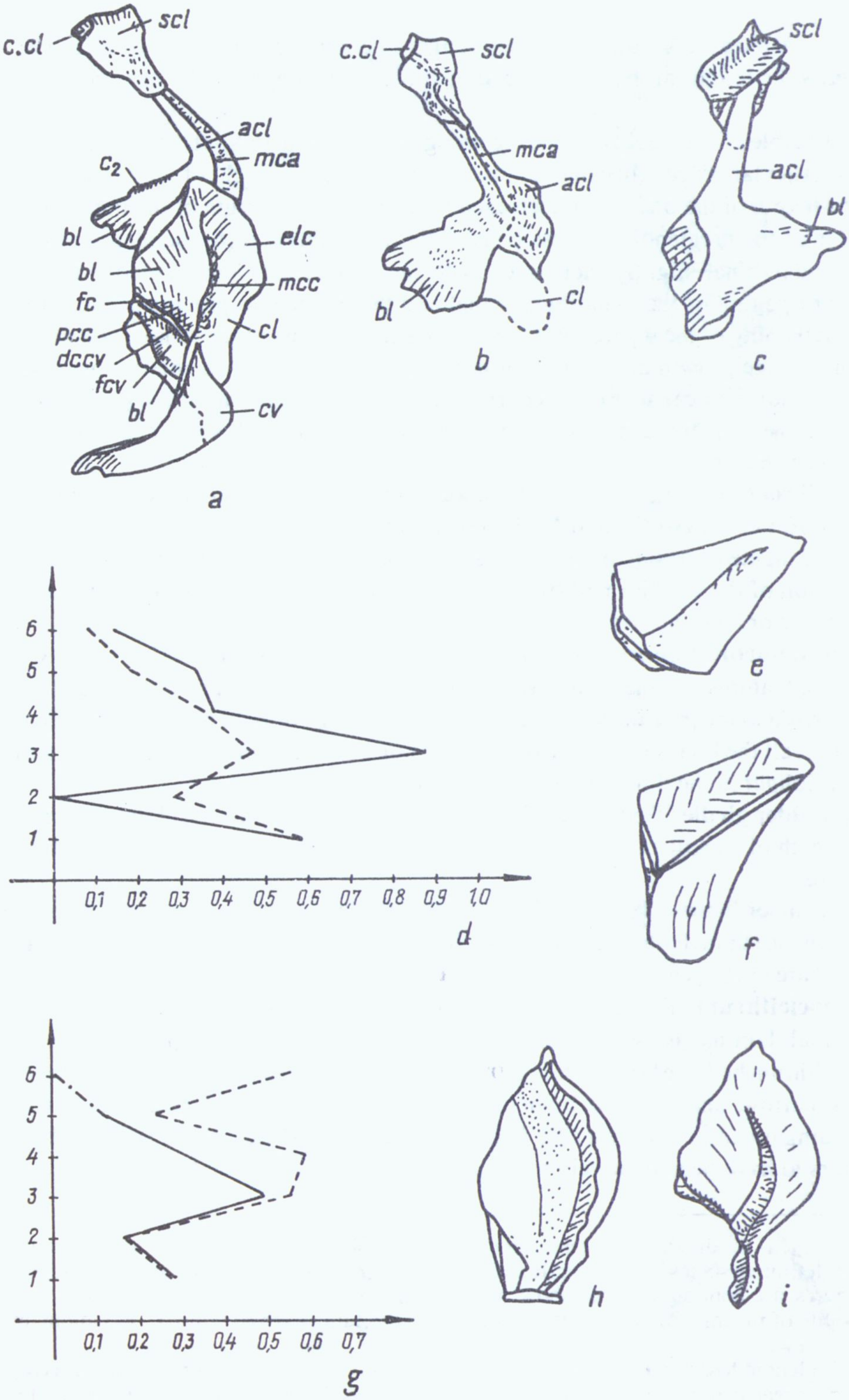
Text-fig. 1. a - the diagram of the parasphenoid growth changes; b - parasphenoid of juvenile and of definitive stages in the juvenile scale; c - the diagram of the mandible growth changes; in figures a-c continuous lines show juvenile and dotted lines definitive stages; d, e - mandible of juvenile (d) and of definitive (e) stages in the juvenile scale; f - mandible, in lateral view.
glen.f - glenoid fossa; m.c - mandibular canal; o.c - oral canal; p.pglen - preglenoid process; p.prart - prearticular process; g, combined schematic skull roof of definitive stage; h, the ethmoid region, in ventral view; i, schematic lower jaw symphysis, in dorsal view.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stage. This bone is reconstructed hypothetically on the base of the contact areas with supracleithrum and cleithrum.

Cleithrum (Text-fig. 2a,g-i; Plate, d). The cleithrum underwent the most essential changes in the process of development. In the juvenile stage it was undeveloped. The cleithrum of adults is a massive bone testifying its importance for muscle attachment. During growth (1) this bone began to curve in the opposite direction and to straighten partially; (2) its external part grew larger in the zone of elc which became gradually as wide as the branchial lamina; (3) the medial crest of the cleithrum (mcc) became almost twice as short in relation to the total length, and relatively higher, its height in the proximal part of the cleithrum in adults being almost 1/4 of its length; (4) the area of branchial lamina (bl) became smaller, but simultaneously the clavicle started to be more depressed owing to the depression of the branchial lamina fc proximal part and enlargement of the crest pcc, which formed the posterolateral edge of the depression fc; (5) the proximal part of the cleithrum became narrower and longer, forming a sufficiently long stem owing to the enlargement of the contact area with the clavicle. In the central part of the stem there is a crest which is the extension of the crest pcc of the cleithrum. This crest separates the marginal part of the cleithrum into outer and inner zones (the latter being the zone of contact with the clavicle).

Clavicle (Text-fig. 2a; Plate, e). During growth, the clavicle became curved in accordance with the enlargement in height and thickness. The proportions between clavicle length and width remained stable. The most important changes took place i0n the contact area with the branchial lamina of the cleithrum. This part of the clavicle is elongated and sharp, having three differently oriented surfaces. The dorsolateral surface reveals a triangular depression (fcv) (on the clavicle of juveniles it is hardly noticeable). The external wall of this depression is formed by the distal crest (dccv) adjacent to the posterolateral crest (pcc) of the cleithrum. The crest is formed by the branchial lamina (bl) that has an irregular margin. During growth the depression (fcv) and its walls enlarged (i.e., the ratio between the length and width of clavicle distal part). On the whole the clavicle became wider and more massive with growth as it assumed a greater functional role.

Pterygoids and pterygoid tooth plates. During growth the proportions of the tooth plates did not change. The plates grew with the addition of denticles on the lingual side of the ridges. The changes took place in the part of the pterygoids lacking the tooth plates. With growth the wing-shaped projections become larger, the areas of jaw-muscle attachments were formed, and widened.

Prearticular tooth plates. The ratio did not change during growth.

Text-fig. 2a-c. Outer shoulder girdle. acl - anocleithrum; bl - branchial lamina; c.cl - contact area with I bone; cl - cleithrum; cv - clavicula; c2 - crest 2; dccv - distal crest of clavicula; elc - external lamina of cleithrum; fc - cleithrum fossa; fcv - clavicle fossa; mca - medial crest of anocleithrum; mcc - medial crest of cleithrum; pcc -posterior crest of cleithrum; scl - supracleithrum; d - the diagram of the supracleithrum growth changes; e, f - supracleithrum of juvenile (e) and of definitive (f) stages in juvenile scale; g - the diagram of the cleithrum growth changes; h, i - cleithrum of juvenile (h) and of definitive (i) stages in the juvenile scale.

Juvenile tooth elements

Symphysis of mandible and dentary tooth plates (Text-fig. 1i). In the juvenile stage, the symphysis of the mandible of *Andreyevichthys epitomus* had a trapeziform cosmine cover which was underlain inside with a thin perichondral bone layer. The cosmine is penetrated with relatively large pores forming a regular pattern. On the ventral side of the posteromedial part of the symphysis, there are elements of the dentition consisting of low denticle rows, laterally flattened, roughly round in outline, and with sharp edges. These elements are unknown in other dipnoans. The rows of denticles radiate from one point and the whole structure looks like a tooth plate. The rows of the dentary tooth plates are greatly elongated laterally. The cosmine disappeared from the dermal bones in the adult stage. In addition, the mandibular symphysis seems to consist of cartilage.

Ethmoid region of skull and the rostral tooth plates (Text-fig. 1h; Plate, h,i). The ethmoid region or hard upper lip is preserved on juvenile specimens as a cosmine cover roughly semicircular in outline. This cover is underlain inside with a thin perichondral bone layer. The cosmine is penetrated with large pores of different sizes, forming a regular pattern. On the ventral side of the external margin of the ethmoid, there are two small tooth plates located close to each other. Rostral tooth plates are known also in *Orlovichthys limnatis* Krupina, in which they are preserved in adult stage (see Novitskaya, Krupina, 1985). Each plate has 3-5 denticles of different development stages. Topographically, and, in some cases, also homologically, the plates correspond to the teeth of rhipidistians and the most primitive dipnoan *Diabolepis speratus* Chang et Yu, 1984 (Smith and Chang, 1990). The anterior external nostril notches are located lateral to these plates. The cosmine disappeared in the adult stage, and, as a result, the ethmoid might have been formed only by cartilage.

Vomerine tooth plates (Plate, f,g). Vomerine tooth plates are very well preserved. The size of the plates varies from 1 to 4 mm. They are relatively flat, slightly arch-shaped, vertically oriented. They are built up of several layers of hard tissue. The base of the plates is formed of spongy bone. Covering the layer of bone, there is a layer of shiny dentine, surrounding a row of laterally flat and sharp teeth. The smallest teeth are situated in the central part of the plate and become larger marginally. Although some plates are bilaterally symmetrical, most of them are not. *Andreyevichthys epitomus* had vomerine tooth plates perhaps only at the juvenile stage, as we have not found such plates in adult stage.

The study of the microstructure of the dentition of juvenile *Andreyevichthys epitomus* has shown that all the tooth plates (dentary, rostral and vomerine) are composed of dentine similar to that of the prearticular and pterygoid plates. The body of a tooth is built up of petrodentine, the walls being composed of trabecular dentine (sensu Denison, 1974) or homogenous compact dentine (sensu Smith, 1977).

Some structures analyzed underwent essential changes during their growth (e.g., parasphenoid, lower jaw, and shoulder girdle), whereas other structures changed their proportions very slightly (e.g., skull roof bones, prearticular and pterygoid tooth plates). Such a difference in the development might be explained by the juvenile underdevelopment of structures as well as by a number of morpho-functional and ecological reasons. One of them is metamorphosis proceeding in ancient fish perhaps the same way as it does in modern fish, without particularly great changes (Kemp, 1986). Another is the change of the mode of life and the feeding mechanism. Great changes took place in the anterior region of the skull or snout. Bones C, E, and M+L_2 and the anterior part of the lower jaw elongated, corresponding to the elongation of the anterior region of the skull. The lower and upper lips of adults were composed of cartilage. The cosmine disappeared from the dermal bones. At the same time the juvenile tooth elements were completely reduced. A transition to bottom- dwelling could induce the intensive development of paired fins.

Some conclusions can be presented on the ecology of *Andreyevichthys.* We believe that the juveniles when feeding used a special juvenile dentition only. Their prearticular and pterygoid plates show no traces of wear. This can be corroborated also by the fact that the jaw muscles were poorly developed (the absence or underdevelopment of areas of muscle attachments on the lower jaw and pterygoids). Juveniles might have been surface- water (plankton and ostracode) feeders. The movement of the lower jaw was probably vertical in order to grip the food. According to our data the adults adopted for life on the bottom when reaching 8 cm or more in length. Their tooth apparatus consisted of paired pterygoid and prearticular tooth plates of *Dipterus*-type (radiate tooth rows). Such plates were used to pierce and grind. Therefore, they could feed on algae and various soft-bodied organisms (e.g., worms). The manner of jaw movement was horizontal (i.e., the lower jaw could move in the angular and front-back directions (lateral directions sensu Campbell and Barwick, 1984).

The sedimentary rocks and fossils in the locality Andreyevka-2 show that the basin inhabited by *Andreyevichthys* was of a lagoonal type.

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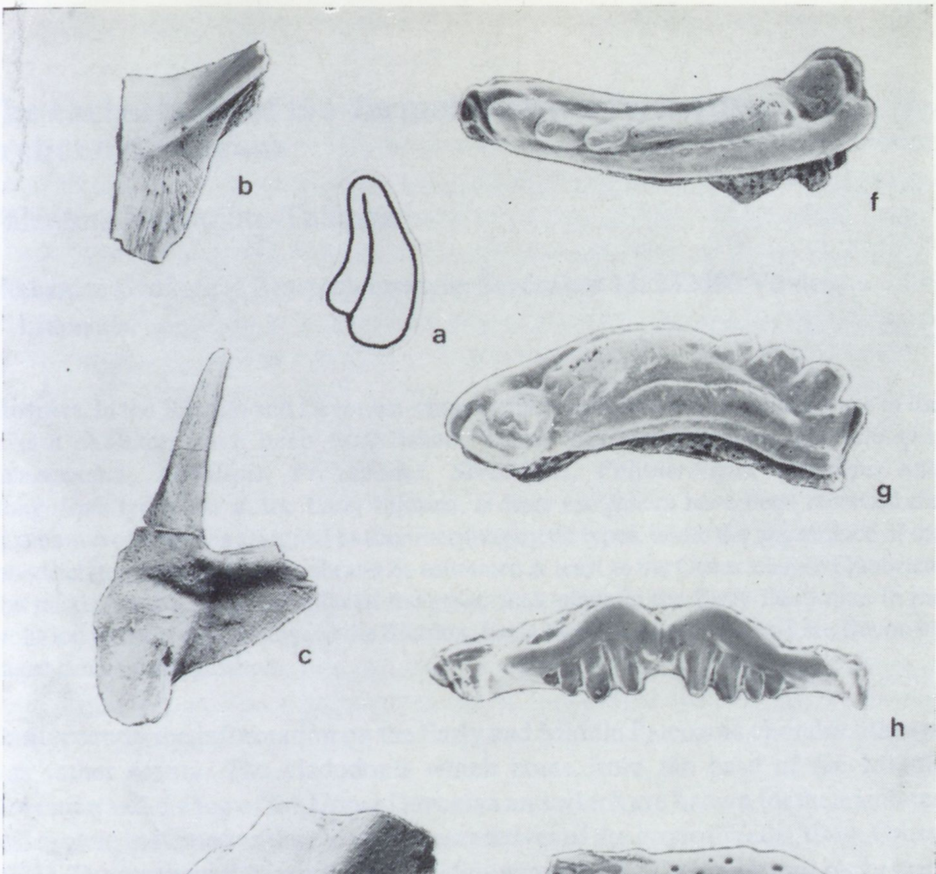
Plate

a - hypothetical anocleithrum; b - supracleithrum; c - anocleithrum; d - cleithrum; e - clavicle. (b-e in natural size); f, g - vomerine tooth plates (4 mm) in dorsal (f) and in lateral (g) view, x50; h - rostral tooth plates (4 mm), in ventral view, x 50; i - rostral tooth plates with cosmine cover (5 mm), in dorsal view, x 30. Photographs f, g, h and i are taken with SEM.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The early stages of the dermal skeleton formation in chondrichthyans

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Abstract. In the Silurian and Devonian chondrichthyans nine morphogenetic types of the dermal skeleton have been established. These are: *Heterodontus*, *Elegestolepis*, *Ctenacanthus*, *Altholepis*, *Protacrodus*, *Seretolepis*, *Polymerolepis*, *Lugalepis* and *Mongolepis* types. As in the Early Silurian, at least six genera have been recorded the squamation of which is assigned to four morphogenetic types, while the appearance of the chondrichthyan gnathostomes should be estimated at least as the Ordovician or Cambrian. The maximum adaptive radiation of the group took place in the Early Devonian. In the evolution of the chondrichthyans the Silurian, Early Devonian and Middle-Late Devonian stages can be distinguished.

Until recently the information on the Early and Middle Paleozoic chondrichthyans was rather scanty. The cladodonts which come from the base of the Middle Devonian and the top of the Upper Devonian and which are known for their isolated scales were indicated as the oldest representatives of the group (Wells, 1944; Gross, 1973). The ctenacantids, particularly widely spread in the Carboniferous rocks were also known as comparatively early forms. Finds of the scales of *Polymerolepis* and *Seretolepis* in the Lochkovian of Podolia (Obruchev and Karatajūte-Talimaa, 1967; Karatajūte-Talimaa, 1977), and *Elegestolepis* in the Upper Silurian of Tuva (Karatajūte-Talimaa, 1973) and Lower Silurian of Siberia (Novitskaya and Karatajūte-Talimaa, 1986) have considerably pushed back in time the appearance of the chondrichthyans. Later on the scales of *Ellesmereia* were recorded from the Lower Devonian of Canadian Arctic (Vieth, 1980), as well as the scales of the hybodontid type (genus *Arauzia*) and the cladodonts (genus *Iberolepis*) from the Lower Devonian of Spain (Mader, 1986).

The collection upon which this paper is based contains mainly the new material. The data on its greatest part have not been published yet. Of the earliest age are tiny scales of the representative of a new genus *Niualepis*, as well as those of *Elegestolepis conica* Kar.-Tal., 1986. They came from the Middle Llandovery rocks of South Yakutia and Bratsk region. The Upper Llandovery of Irkutsk amphitheatre, Tuva and North Mongolia has also yielded a highly interesting material. It comprises the new species of the genera *Elegestolepis* and *Polymerolepis* (?), as well as the new genera *Mongolepis*, *Udalepis* and *Sodolepis* attributed to a new order, or maybe a new taxon of a higher rank. Different types of scales are especially numerous in the Lower Devonian (Lochkovian) of Podolia. Besides the remains of the above mentioned forms, the isolated scales of the representatives of

Altholepis, *Kneria*, and two new genera (no. 1 and 2) have been found. Rather primitive scales of the "cladodonts" were discovered in the Emsian of East Pamyr (genus *Pamyrolepis*). Solitary scales of ctenacantids can sometimes be met in the Lower Devonian of Podolia, Timan-Pechora Region, Taimyr and Pamyr. It is very difficult to identify them even to the generic level. The scales undoubtedly belonging to *Ctenacanthus* and to a representative of a new genus no. 3 occur in the upper part of the Upper Devonian and the lower parts of the Carboniferous of Timan-Pechora Region. For comparison the scales of *Ctenacanthus* coming from the lower part of the Carboniferous of the Moscow Region (environs of Serpukhov, A. Ivanov's collection have been studied). One should also mention the genus *Lugalepis*. A large portion of the squamation of this fish was found in the Ventspils boring, Latvia, in the upper part of the Lower Devonian. Isolated scales of the same form were recorded in the Narva Formation of the Leningrad Region (Luga River), and Lithuania.

All these forms listed above needed to be classified. At least an approximate place should be found for them in the classification of the chondrichthyans. Also, a method for determining the taxa of various ranks should be worked out. Systematics of the chondrichthyans, which are known only by their isolated scales, is poorly developed and their assignment to the orders is not always reliable (Zangerl, 1981).

Methods for the identification of the scales of the chondrichthyans (elasmobranchs) are elaborated owing to the investigations by Stensiö, Gross, Ørvig, Zangerl and Reif. However, these studies concern mainly the Mesozoic and Cenozoic forms. As an impulse for work in this field served the famous Stensiö's lepidomorial theory (Stensiö, 1961) based on the scales of the Upper Permian edestids. Although the main conclusions of this theory appeared to be erroneous, and later were rejected even by Ørvig, the co-author, in our opinion the theory has a lot of rational aspects. The term "lepidomorium" or "unit", as the main element of the dermal skeleton of vertebrates below tetrapod level, is the precursor of the term "odontode" suggested by Ørvig (1967). From the principles of cyclomorial growth and synchronomorial scale formation originated the terms "growing" and "non-growing" scales introduced by Reif. Stensiö gave a detailed description of all morphologic changes that took place during the ontogenetic development of the scales of cyclomorial and synchronomorial types.

Of great importance in the study of the skeleton formation in lower vertebrates was the work published by Ørvig in 1977. The conception of an odontode was worked out, its growth scheme was outlined, and its exceptional roie in the formation of the dermal skeleton was proved. Here this conception is appropriated and a short definition of the odontode is given according to Ørvig. An odontode is formed ontogenetically from a single, undivided dental papilla of the mesenchymal soft tissue bounded at its circumference by an epithelial dental organ in the adjoining epidermis. It consists of dentine or, in some forms, of dentinous tissue; it frequently possesses a superficial enameloid layer and does not belong to the dentition sensu stricto.

In 1982 Reif published his odontode regulation theory which can be considered as a further stage in the development of Ørvig's odontodic conception. It was based on the morphogenetic and regulation processes observed in living and fossil vertebrates. Reif considered also teeth as odontodes.

Gross (1973) suggested that the earliest chondrichthyans had teeth little differing from the scales in their and structure. This seems to be true, because up to now teeth of the chondrichthyans have not been found in the Silurian and Early Devonian rocks. Teeth discovered in the Middle and Upper Devonian belong to "cladodontic" type.

Before discussing the morphogenetic squamation types of the Paleozoic chondrichthyans, it would be reasonable to consider the principal structure of the scales of various types.

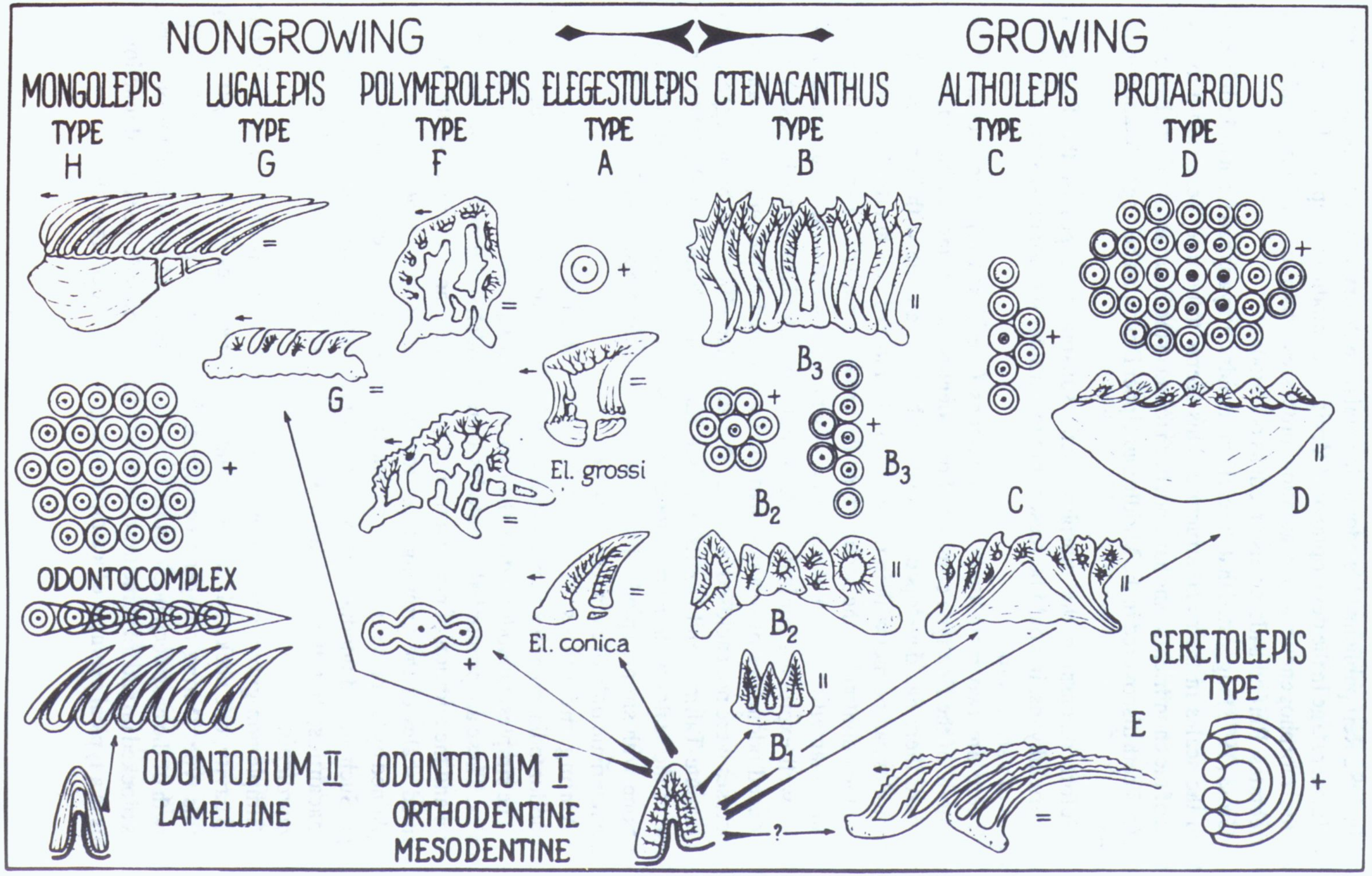
There are two main types of odontodes (see Text-fig.). The crown of the odontode of the first type consists of orthodentine, sometimes of mesodentine. In the base there has developed an acellular bone or a bone with bone cells. Such odontodes can be met with in the scales of the most of the chondrichthyans.

In the odontode of the second type the crown consists of a specific dentinoid tissue — lamelline or atubular dentine — which has no dentine tubules and shows only well-expressed lamination. Apparently odontoblasts (lamelloblasts) which produced odontodes of this type had totally retreated to the pulp cavity and their processes were not enclosed in tissue. The term "lamelline" has been suggested by Karatajūte-Talimaa and Novitskaya (see Karatajūte-Talimaa et al., 1990). In the base of the scales with the odontodes of the second type, the acellular bone tissue or bone with simple spindle-like bone cells had developed. Such odontodes are characteristic only of mongolepid scales.

Among the scales of the Paleozoic chondrichthyans occur simple monodontodia, complex monodontodia and polyodontodia of different geneses.

The simplest monodontodia can be found in the squamation among the growing scales. These are primordial odontodes around which the growing scales started to form and the addition of new odontodes took place. The occurrence of the already formed scales of the growing type, together with simple monodontodia, can be explained by later insertion of the monodontodia among larger scales of the growing type. Such monodontodia are especially characteristic of hybodontoids and, maybe, ctenacantids, but they are also known in the most primitive "cladodont" *Pamyrolepis.*

Simple non-growing monodontodium (type A) consists of the crown with one pulp cavity, one neck and one basal canal. E.g., the scales of *Elegestolepis* belong to this type. During ontogeny centripetal filling up the pulp cavity and gradual growth of the base deep into corium took place. The basal opening of the old scales was blocked up and for some time, until they fell out, only the neck canal functioned. This is a typical example of a simple non-growing, shedding scale.


NONGROWING
GROWING
MONGOLEPIS TYPE H
LUGALEPIS TYPE G
POLYMEROLEPIS TYPE F
ELEGESTOLEPIS TYPE A
CTENACANTHUS TYPE B
ALTHOLEPIS TYPE C
PROTACRODUS TYPE D
=
+
G =
El. grossi
El. conica
B3
B2
B1
C
D
ODONTOCOMPLEX
SERETOLEPIS TYPE
E
ODONTODIUM II
LAMELLINE
ODONTODIUM I
ORTHODENTINE
MESODENTINE
?

Complex monodontodia are found in non-growing scales of the *Polymerolepis* type. The crown is covered with a continuous layer of orthodentine, and the pulp cavity is divided into numerous cavities. A great number of neck and basal openings, a poorly developed ring-like base of a complicated outline fully conform to the "synchronomorial" type of the scales by E. Stensiö. Complex monodontodia most likely occurred on the head of an animal. The fusion of the odontodes into one conical or fungoid crown took place before mineralization.

Polyodontodia of non-growing scales of the Polymerolepis type were formed in the same way. Depending on their location on the body, already in a papillar stage, many odontodes fused into one scale of a definite shape. Their tops were detached, and the whole crown was covered with a continuous thin layer of orthodentine. The pulp cavity was divided into numerous cavities, the thin concave base was penetrated with numerous basal openings, and the neck region bore neck-canal openings.

Polyodontodia of the growing scales were formed by the addition of new odontodes to the already existing ones. This may have taken place in various ways: in type B on the sides, on the sides and on the front and areally; in type C on the sides, on the sides and on the back; in type D areally; in type E areally and half-areally.

The B-type scales have a poorly developed ring-like base, in the B_1 subtype the base is slightly convex.

The C-type scales have a concave, but a massive base deeply penetrating into scale body and conical in cross-section.

All "cladodontic" scales belong to type D. Their odontodes are approximately of the same size and had been added areally, forming rather regular ring-like zones. The base is convex, growing evenly.

Particular scale-like polyodontodia are characteristic of the E- type scales. Here odontodes are grouped into special leaf-like plates or odontocomplexes. Small plates are in the front part of the scale, and the subsequent ones, larger and larger, appear under these in the front. Addition of leaf-like plates takes place from below and is not always regular. The base is small and concave.

The polyodontodia of synchronous origin are formed in a totally different way. To type G, flat diamond-shaped frequently asymmetric scales are attributed. Their crown consists of several or many odontodes of approximately equal size and shape (genus *Lugalepis*). The odontodes are situated irregularly or arranged in somewhat longitudinal rows.

Type H is represented in the scales of all mongolepids. The scales, i.e. polyodontodia of synchronous origin, consist of a system of longitudinal odontocomplexes. Each odontocomplex includes a larger or smaller number of

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Morphogenetic types of scales in Paleozoic chondrichthyans. Crosses (+) mark diagrammatic parabasal sections of odontodia, vertical lines (||) vertical transverse sections of scales, horizontal lines (=) vertical longitudinal sections of scales, arrows anterior end of scales.

odontodes, with their tops curved back and leaning on the odontodes behind them. Comparatively large and not numerous odontodes form the odontocomplexes of *Sodolepis*. The odontocomplexes of *Udalepis* consist of more numerous small and low odontodes. The scales of *Mongolepis* have the most complicated structure: odontocomplexes consist of a huge number of small and high odontodes. The base of the scales of all mongolepids grew downwards into the corium during the ontogenetic development. It consisted of the acellular bone tissue (in *Mongolepis*, *Sodolepis*), or bone tissue with numerous bone cells (in *Udalepis*).

While establishing the morphogenetic types of squamations of sharks and other elasmobranchs, Reif (1978, 1980) took into account four parameters: shedding, growth of the scales, increase in size of odontodes and an increase in the number of scales in the squamation. Thus he distinguished six morphogenetic squamation types of elasmobranchs. Four types concern also several Paleozoic chondrichthyans: *Heterodontus*, *Protacrodus*, *Ctenacanthus costellatus* and *Hybodus delabechei*.

Non-growing scales

***Heterodontus* type** includes "placoid" scales proper, characteristic of euselachians, which were non-growing, shedding and replaced. Growth of the skin was compensated by the gradual increase in the size of the replacement scales and the addition of the new ones. In the Upper Devonian "placoid" scales of an uncertain origin are very rare.

The following three types are characteristic of the Lower and Middle Paleozoic chondrichthyans. ***Elegestolepis* type** is the simplest morphogenetic type of the squamation. The scales were non-growing, shedding and replaced with larger ones. Growth of the skin was compensated by the increasing size of the replacement-scales and the addition of the new ones. The total number of the scales increased during the ontogenetic development of an animal in the same way as in euselachians the dermal skeleton of which consists of non-growing scales of the "placoid" type. Genera *Elegestolepis* and *Ellesmereia.*

Growing scales

***Ctenacanthus* type.** The squamation consists of simple monodontodia and growing polyodontodia. The base of the scales was poorly developed. Growth of the scales took place by means of adding new odontodes on the sides of the primordial odontode, areally around it, and also on the sides and at the front. Accordingly, morphologic subtypes B_1, B_2 and B_3 of the scales are distinguished. Subtype B_1 is the simplest, the odontodes are few in number and detached (genus *Niualepis*). In subtype B_2 the scales were of the hybodontid type, the addition of the odontodes was areal, growth irregular (genus *Arauzia*). Subtype B_3 scales grew more regularly. The odontodes were detached (genus *Ctenacanthus*).

Growth of the skin in the morphogenetic *Ctenacanthus* type was compensated with the growth of the scales and with the addition of new scales. Therefore the squamation consisted of scales of various age stages with a different number of odontodes. The total number of the scales increased during the ontogenetic development of an animal.

The *Hybodus* type is included into the *Ctenacanthus* type, and it remains problematic in morphogenetic aspect. According Reif, the hybodontids had both growing and non-growing scales in the same part of the skin. If simple odontodes are attributed to non-growing scales, from which the actual formation of any growing scale begins, such co-occurrence quite corresponds to the situation in *Ctenacanthus*. Yet, if we consider "placoid" scales as non-growing scales that are more complicated than simple odontodes, their vicinity to the growing scales is hard to explain.

***Altholepis* type.** The squamation consisted of polyodontodia, i.e. growing scales. The base was concave. Addition of odontodes took place on the sides and on the back. Growth was regular, the scales were non-shedding. Evidently the growth of the skin was compensated only by the scale growth. Most likely during the ontogenetic development the total number of the scales remained rather constant. Genera *Altholepis*, *Iberolepis*, gen. n. 1 and gen. n. 3.

***Protacrodus* type.** The squamation consisted of polyodontodia, i.e. of growing scales with a convex base. The squamation of the Early Devonian genus *Pamyrolepis* contained some monodontodia. An addition of odontodes and an increase in the base took place regularly and areally. The scales were non-shedding. Growth of the skin was compensated only by the scale growth. During the ontogenetic development of an animal the total number of the scales remained constant. Genera *Ohiolepis*, *Pamyrolepis*, *Cladolepis*, *Maplemillia*, *Hercynolepis*, *Protacrodus*, etc.

***Seretolepis* type.** The squamation consisted of polyodontodia of areal and half-areal growth. The base is small and concave. The addition of odontodes was not always regular. Apparently in the squamation not only growth of scales but also addition of the new scales took place, therefore during the ontogenetic development of an animal the total number of the scales increased. Genera *Seretolepis* and *Kneria*.

Non-growing scales

***Polymerolepis* type.** The squamation consisted of complex monodontodia and polyodontodia of synchronous origin. As all non- growing scales, they were shedding and replaced by larger ones; the shape of scales depended on their location on the body. There can be distinguished head (complex monodontodia), body (polyodontodia with a variable number of sections) and tail (more monolithic, leaf-like) scales. Growth of the skin was compensated by the growth of the replacement scales and the addition of the new scales. The total number of the scales increased during the ontogenetic development of an animal. Genus *Polymerolepis*.

***Lugalepis* type.** The squamation consisted of polyodontodia of synchronous origin. The number of the odontodes and the shape of the scales depended on their location on the body. The base was thin, slightly concave. The scales were shedding and replaced, the growth of the skin was compensated by the increase of replacement-scales. Addition of new scales was also possible. In this case during the ontogenetic development of an animal the number of scales could increase. Genus *Lugalepis*.

***Mongolepis* type.** The squamation consisted of polyodontodia of synchronous origin forming a system of odontocomplexes. The crown was of the non-growing type. The base was growing. During the ontogenetic development of an animal, in the squamation shedding and replacement of the scales by the bigger ones took place as the compensation of the growth of the skin. It is hard to decide whether the scales were added and whether their total number increased. Genera *Mongolepis*, *Sodolepis*, *Udalepis* and gen. n. 2 (?).

As at least nine types of the dermal skeleton can be distinguished in the Silurian and Devonian chondrichthyans, evidently there existed a great variety of forms of different systematic positions. Undoubtedly they formed a prosperous group of the lower vertebrates, well adapted to the life in the coastal waters of epicontinental sea basins. Judging by the fact that in the Early Silurian no less than six genera have been recorded the squamations of which are represented by four morphogenetic types, the time of the appearance of the chondrichthyans could be pushed back to at least Ordovician or Cambrian. The maximum of the adaptive radiation of the group falls into the Early Devonian, when genera, characteristic only of this period existed and the euselachians — ctenacantids, hybodontids and protacrodontids ("cladodontids") appeared. In the development of the chondrichthyans, the Silurian, Early Devonian and Middle-Upper Devonian stages could be distinguished.

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Early Devonian actinopterygians (Osteichthyes, Pisces) from Siberia.

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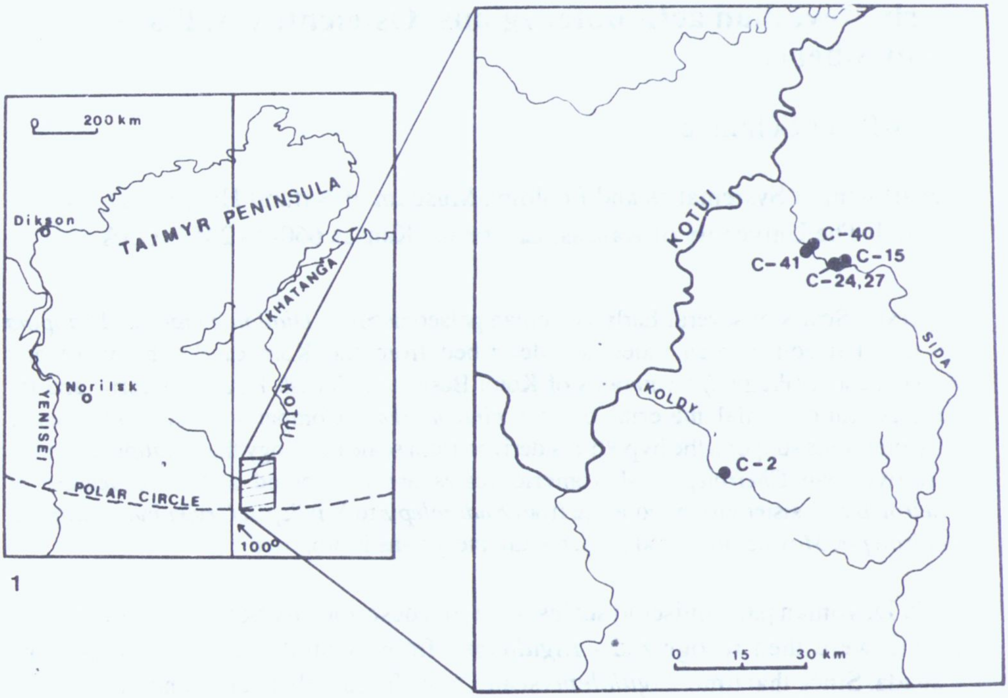
Abstract. Scales of several Early Devonian palaeoniscoids, *Dialipina markae*, *Dialipina* sp. and Palaeoniscoidea indet. are described from the Kureika (Lochkovian) and Razvedoohnyi (Pragian) formations of Kotui Basin and Norilsk Region, Siberia, and for the first time cranial material of *Dialipina markae*. Comparison with other early palaeoniscoids supports the hypothesis derived from scale histology that *Dialipina* is more primitive than *Cheirolepis*. Micromeric scales are considered a derived feature of *Cheirolepis*. A sister group sequence from *Andreolepis* to *Naxilepis*, *Orvikuina*, *Dialipina*, *Cheirolepis*, *Moythomasia* and higher actinopterygians is proposed.

Early Devonian palaeoniscoid scales were first described by Schultze in 1968. Two genera were then recognized - *Ligulalepis* from Australia, and *Dialipina* from Canada. Since that time, *Ligulalepis* scales have frequently been found in Australia at a number of sites in rocks of Pragian and Emsian age (Giffin, 1980; Turner et al., 1981; Turner, 1982). Wang and Dong (1989) recently described scales of *Ligulalepis* and of a new genus, *Naxilepis*, from the Qujing district, Yunnan Province, Southern China. A second occurrence of *Dialipina* scales was recorded by Mark-Kurik (1974) and Schultze (1977) from the Gedinnian of Kotelny Island, New Siberian Archipelago.

Despite these occurrences of scales, no cranial material of any Early Devonian palaeoniscoid had ever been found until 1976, when Mrs. S. Konstantinova discovered new material of *Dialipina* in the Kotui Basin (Text-figs. 1, 2), Siberia, that for the first time included bones other than scales. These bones will be described here, along with scales of the same age from the Norilsk region. The material will be compared with other early palaeoniscoids, in particular *Moythomasia*, *Mimia*, *Cheirolepis* and *Andreolepis*. *Andreolepis* is the earliest known actinopterygian (Gross, 1968; Schultze, 1977; Janvier, 1971, 1978) from the uppermost Lower or Middle Ludlovian (Upper Silurian) of Gotland, Sweden.

I would like to express my sincere thanks to E. Kurik, Institute of Geology, Academy of Sciences of Estonia, Tallinn, who offered me the material (with prefix Pi) for description and kindly supplied all of the data on localities and stratigraphy. Dr. J. Chorn, Museum of Natural History, The University of Kansas, Lawrence, Kansas, prepared the photographs; M. Gottfried, also from the Museum of Natural History, revised the English and gave helpful comments. Ms. J. Elder, Division of Biological Sciences, The University of Kansas, Lawrence, Kansas, typed the manuscript. I would like to thank them for their kind help.



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Text-fig. 1. Location of Norilsk and the Kotui Basin, Siberia.
Text-fig. 2. Kotui Basin, Siberia.

Description

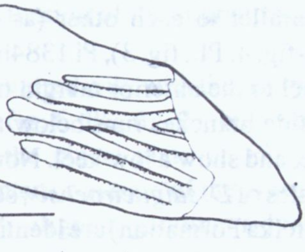
Actinopterygii, **Palaeoniscoidea,** indet.

Material. Pi 1390, Pi 1391 (scales in internal view); Pi 1392 (deep scale).

Horizon and locality. Pi 1390 and 1391, upper part of Kureika Formation, Lochkovian, Lower Devonian (according to Cherkesova, 1988), bore hole T-132: 901 and 904.5 m depth; Pi 1392, basal part of Razvedochnyi Formation, Pragian, Lower Devonian, borehole T-140, 1450.6 m depth, Norilsk region, Siberia.

Scales. The two scales (Pi 1390 and 1391) are preserved in internal view and originated from the caudal or the ventral abdominal region. The narrow ridge on the anterior half of the inside surface indicates that they are palaeoniscoid scales; a more precise identification is not possible.

The deep scale Pi 1392 (Text-fig. 3) is from the anterior abdominal region and is preserved in lateral view. It possesses a pronounced peg with a narrow base. The anterodorsal corner forms a right angle, whereas the posterodorsal and anteroventral corners are more rounded. The posterior margin is serrated, with the four most ventral serrations being virtually identical. Each of these serrations continues



Text-fig. 3. Palaeoniscoid indet., scale of anterior abdominal region; Pi 1392. x 38.5. Basal part of Razvedochnyi Formation, Pragian, D1; Norilsk region, Siberia.
Text-fig. 4. *Dialipina markae*, scale of dorsal or ventral abdominal or caudal region; Pi 1384 a. Lower member of Kureika Formation, Lochkovian, D1; locality C - 15, sample C-15/10, Sida River, Kotui Basin, Siberia. Arrow points anteriorly. Scale equals 1 mm.

anteriorly as a shallow ridge, which then turns dorsally to parallel the anterior margin. The ridges represent sequential growth stages.

Dorsal to the four large serrations is a shorter serration set in an invagination of the posterior margin; this invagination may indicate that it is a lateral line scale, although an opening is not visible. Another pointed serration is positioned above the invagination; it bears an elevated, anterodorsally extended ridge.

The deep scale belongs to an undescribed early Devonian palaeoniscoid. It is distinct from *Dialipina* scales in that the ridges are not separated from each other, and intercalating short ganoin ridges are not present at the posterior margin as they are on *Dialipina*. Instead, each new ridge is added close to the preceding one. While the material is too limited to justify naming a new taxon, the scale does demonstrate that palaeoniscoids were already relatively diverse by the early Devonian.

Palaeoniscoidea
Genus *Dialipina* Schultze, 1968

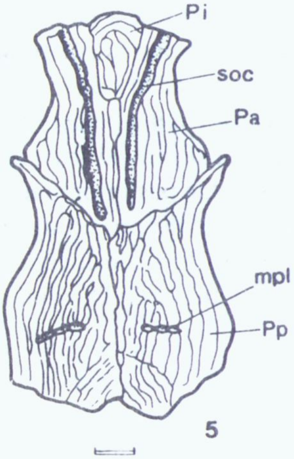
Material. Pi 1381 (cleithrum), Pi 1382 (scale), Pi 1383 (anterior skull roof), Pi 1384 (posterior skull roof), Pi 1384 a, b (two scales), Pi 1385 a-c (three scales), Pi 1386 a-c (six scales), Pi 1387 (one scale), Pi 1388 (one scale), Pi 1389 (four scales).

Horizon and locality. Pi 1381-1382, upper part of lower member, Kureika Formation, Lochkovian, D1; Koldy River, Kotui Basin, Siberia. Pi 1383-1387, lower member, Pi 1388, upper member, Kureika Formation, Lochkovian, D1; Sida River, Kotui Basin, Siberia. Pi 1389, basal beds of Razvedochnyi Formation, Pragian, Lower Devonian; Sida River, Kotui Basin, Siberia. (Age assignments following Cherkesova, 1988).

Scales. The scales show parallel ganoin ridges separated by grooves from each other as seen on *Dialipina.* Intercalated short ganoin ridges at the posterior margin (which are very typical for *Dialipina*) are rarely found on these scales. The ridges run parallel to each other (as on the scales of D. markae) on scales Pi 1384a (Text-fig. 4; Pl., fig. 3), Pi 1384b, Pi 1386a, b and Pi 1382. The ridges turn anteriorly parallel to the anterior margin on scales Pi 1387 and Pi 1389; a longitudinal canal with side branches runs below the ridges. The other scales are seen only from the inside, and show a low keel. None of the scales possesses a pronounced peg as seen on scales of *D. salgueiroensis*; scales Pi 1384-1386 (lower portion of lower member of Kureika Formation) are identified as *D. markae* based on the features cited above.

The scales Pi 1387-1389, higher in the section (higher part of lower member of Kureika Formation, and Razvedochnyi Formation), are assigned to *Dialipina* sp., whereas the anterior portion of the ridges run parallel to the anterior margin on these scales, as in *D. salgueiroensis,* other characteristic features of that species (such as a pronounced peg) are not present.

Skull roofs. Skull roof Pi 1384 occurs at the same locality and in the same horizon together with scales of *D. markae*. The skull roofs Pi 1384 and 1383 are covered by longitudinal smooth ridges similar to the ornamentation on scales of *D. markae*. This, together with the fact that Pi 1384 co-occurs with the scales of that form, suggests that the two skull roofs belong to D. markae.



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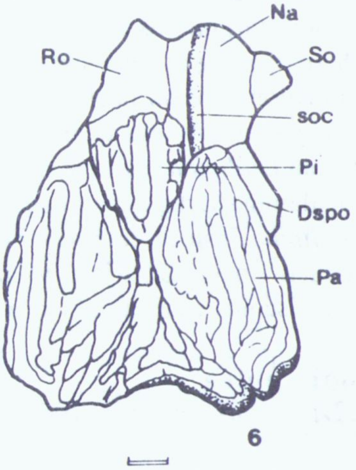

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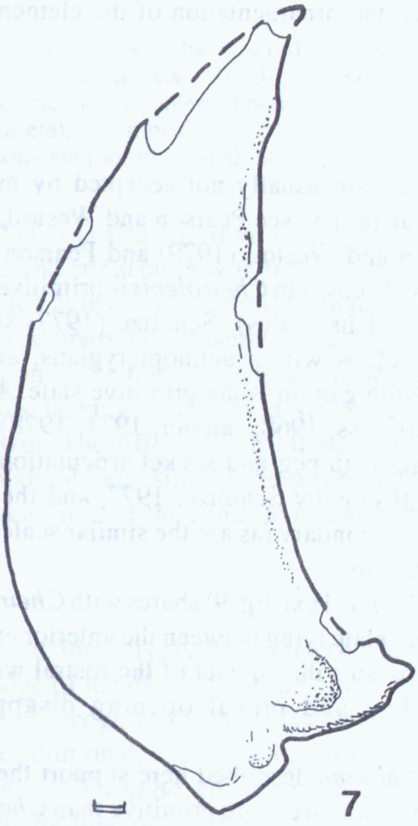
Text-fig. 5. *Dialipina markae*, posterior skull roof; Pi 1384. x 6. Lower member of Kureika Formation, Lochkovian, D1; locality C-15, sample, C-15/10, Sida River, Kotui Basin, Siberia.

Text-fig. 6. *Dialipina markae*, anterior skull roof; Pi 1383. x 6. Lower member of Kureika Formation, Lochkovian, D1; locality C-27, sample C-27/7, Sida River, Kotui Basin, Siberia. Dspo - supraorbitodermosphenotic, mpl - middle pitline, Na - nasal, Pa - parietal (=frontal of commonly used actinopterygian nomenclature), Pi - pineal, Pp - postparietal (=parietal of commonly used actinopterygian nomenclature), Ro - rostral, So - supraorbital, soc-supraorbital canal. Scale equals 1 mm.

Skull roof Pi 1384 (Text-fig. 5; Pl., fig. 1) consists of (using the terminology of Jollie, 1962) paired postparietals (= parietals of more commonly used actinopterygian nomenclature), parietals (= frontals of more commonly used nomenclature) and a pineal plate. The postparietal of Pi 1384 is longer than wide, and has an anterolateral extension beyond the lateral extent of the parietal. It carries the middle pitline; the posterior pitline and the extension of the supraorbital canal into the postparietal are not visible.

Posteriorly, the parietal of Pi 1384 is wide and sutured only with the postparietal. It narrows anteriorly on specimen Pi 1383 (Text-fig. 6; Pl., fig. 2), but appears to be relatively wide near the anterior margin of the pineal plate on Pi 1384. In specimen Pi 1383, the parietals do not reach the anterior margin of the pineal plate. The parietals of both specimens bear closely aligned ganoine ridges. The



Text-fig. 7. ?*Dialipina*, left cleithrum, internal view; Pi 1381. x3. Upper part of lower member of Kureika Formation, Lochkovian, D1; locality C-2, sample C-2/a, Koldy River, Siberia. Scale equals 1 mm.

supraorbital canal runs through the nasal just lateral to the pineal plate, and then through the parietal near the midline.

The pineal plate of both skull roofs forms a triangle with a wide anterior margin. It is covered with closely aligned ridges, and lacks an external pineal opening. A rostral plate lies anterior to the pineal plate, but does not meet the parietals. The nasal lies anterior to the parietal. The anterior narrow portion of the right supraorbitodermosphenotic is preserved; it forms the dorsal margin of the orbit, and reaches anteriorly to the nasal. Lateral to the right nasal, a piece of a bone may represent the posterior portion of a supraorbital.

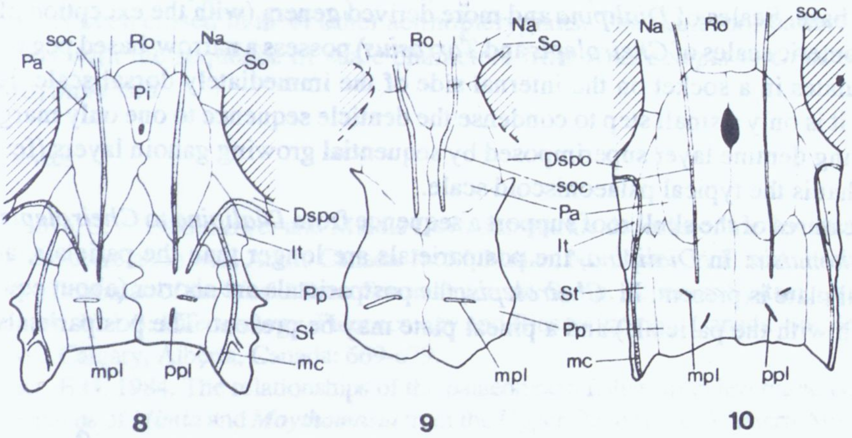
Cleithrum. A strongly weathered bone with the shape of a cleithrum (Pi 1381; Text-fig. 7; Pl., fig. 4) was collected in the Kureika Formation at the Koldy River, Siberia. It is semilunate in shape, with a stout ventral end composed of relatively thick bone. Too little of the scapulocoracoid is preserved to construct its shape. Tentative assignment of the cleithrum (?) to *Dialipina* is based on its co-occurrence with scales of that genus; the ornamentation of the element is unfortunately not preserved.

Comparisons

Scale shape and histology are usually not accepted by most authors as strong evidence for systematic affinities (see Pearson and Westoll, 1979; Pearson, 1982; Gardiner, 1984). Pearson and Westoll (1979) and Pearson (1982) argue that the micromeric state of the scale cover in *Cheirolepis* is primitive (despite the advanced histological composition of its scales). Schultze (1977) showed, however, that multilayered ganoin develops within actinopterygians, and that possession of separate dentine ridges with ganoin is the primitive state. *Andreolepis*, the oldest known actinopterygian (Gross, 1968; Janvier, 1971, 1978), has ganoin on a few ridges. The rhombic scale with peg-and-socket articulation was considered to be primitive within osteichthyans by Schultze, 1977, and the micromeric scales of *Cheirolepis* are therefore secondary (as are the similar scales of the Carboniferous genus *Tarrasius*), not primitive.

The skull roof of *Dialipina* (Text-fig. 9) shares with *Cheirolepis trailli* (Text-fig. 8) the presence of a pineal plate lying between the anterior ends of the parietal. The pineal plate limits or separates the contact of the rostral with the parietal in both genera. The pineal plate and pineal opening disappear in more recent palaeoniscoids.

The skull roofs of *Dialipina* described here support the hypothesis that these Early Devonian palaeoniscoids are more primitive than *Cheirolepis* (Text-fig. 11). *C. trailli* has long postparietals in comparison to the parietals or of equal size, but they are longer still in *Dialipina*. The postparietals are much shorter than the parietals in more recent actinopterygians. A proportionally long postparietal is a primitive feature within osteichthyans as it also occurs in primitive sarcopterygians.



Text-figs. 8-10. Skull roof of Devonian palaeoniscoids. 8 - *Cheirolepis trailli* after Pearson and Westoll (1979); 9 - *Dialipina markae*; 10 - *Moythomasia nitida* after Jessen (1968). Dspo - supraorbitodermos-phenotic, It - intertemporal, mc - main lateral canal, mpl - middle piline, Na - nasal, Pa - parietal, Pi - pineal, Pp - postparietal, ppl - posterior pitline, Ro - rostral, So-supraorbital, soc - supraorbital canal, St - supratemporal.

The presence of a pineal plate is also primitive within osteichthyans, as is the course of the supraorbital canal (no connection with infraorbital canal).

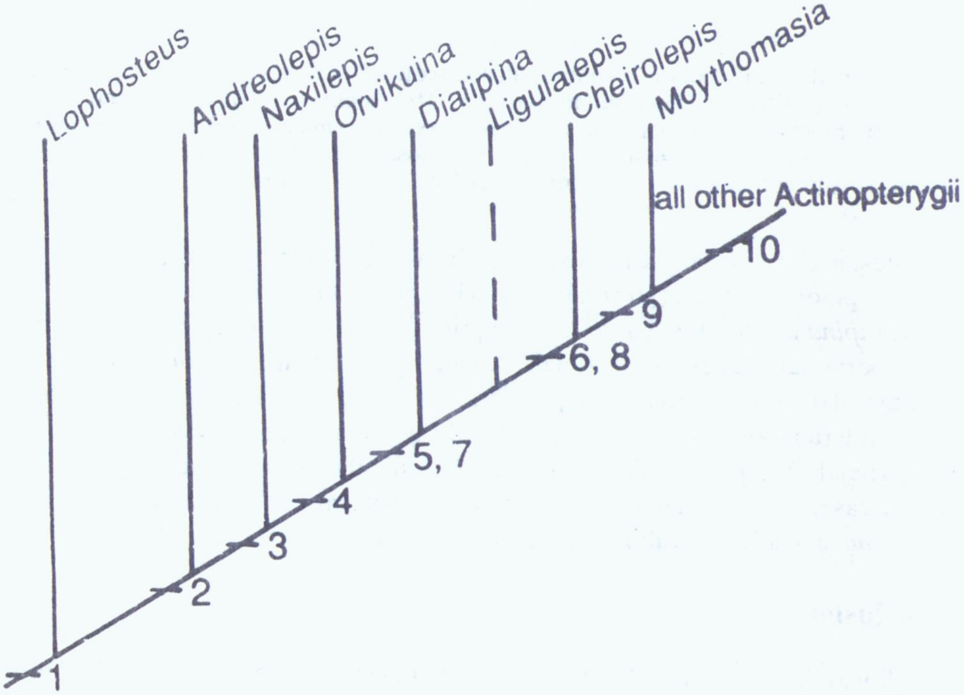
Dialipina is interpreted here as more primitive than *Cheirolepis* on the basis of its proportionally longer postparietals. Assuming that an intertemporal was present, the anterolateral extension of the postparietals would separate it from the parietal. If the intertemporal was lacking, and only a supratemporal was lateral to the postparietal, *Dialipina* would be different from all other primitive actinopterygians. In any case, the anterolateral extension of the postparietal is a unique feature of *Dialipina*, and allows skull roof of the genus to be easily recognized.

Conclusions

Additional finds of early actinopterygians over the last 20 years have resulted in an increase in our knowledge of the diversity of the group during its early evolution. At present, five genera are recognized in the Early Devonian and Late Silurian. All of these genera and one additional, unnamed form are represented by scales; skull roofing bones of one genus, *Dialipina*, are described here for the first time.

Scale histology and morphology support a sequence from *Andreolepis* to *Moythomasia* (Text-fig. 11). *Andreolepis* can be considered an actinopterygian because it occasionally possesses ganoin on its dentine denticles, a feature missing in *Lophosteus*. In the new Silurian genus *Naxilepis*, the anterodorsal corner is elongated (Wang and Dong, 1989; Figs. 5a, b, Pl. 4; Figs. A - D). Ganoin is formed, and each dentine denticle has a bone base with bone cell lacunae. In *Orvikuina*, the denticles are formed by dentine only; bone is restricted to the lamellar bone of the scale base. Scales of *Dialipina* and more derived genera (with the exception of the micromeric scales of *Cheirolepis* and *Tarrasius*) possess a narrow-based peg which articulates in a socket on the internal side of the immediately dorsal scale. From there it is only a small step to condense the denticle sequence to one only marginal growing dentine layer superimposed by sequential growing ganoin layers (feature 6). That is the typical palaeoniscoid scale.

Features of the skull roof support a sequence from *Dialipina* to *Cheirolepis* and *Moythomasia*. In *Dialipina*, the postparietals are longer than the parietals, and a pineal plate is present. In *Cheirolepis*, the postparietals are shorter (about equal in length with the parietals) and a pineal plate may be present. The postparietals are



Text-fig. 11. Phylogenetic sequence of early actinopterygians, mainly after scale features. 1-6 - primitive scale features: 1 - rhombic shape of scale, overlying sequence of dentine denticles and cancellous bone over lamellar bone, 2 - occasional ganoin cover of dentine denticles, 3 - anterodorsal process, ganoin on dentine denticles, 4 - overlying sequences of dentine denticles without bony base, 5 - peg-socket articulation, peg with narrow base, 6 - ganoin layer directly overlying other ganoin layer; 7-10 - primitive skull roof features: 7 - postparietals longer than parietals, pineal plate present, 8 - postparietals equal in length with parietals or somewhat shorter, 9 - postparietals shorter than parietals, loss of pineal plate, 10 - postparietals much shorter than parietals (less than half the length of parietals), pineal foramen closed in most. Autapomorphies of the genera in their morphology.

shorter (feature 9) or much shorter (feature 10) than the parietal in more advanced primitive actinopterygians. The pineal plate is lost (feature 9), and the pineal foramen is even closed in most other actinopterygians. The skull roof pattern thus conforms with the sequence of scale characters from *Andreolepis* to *Cheirolepis* and *Moythomasia*.

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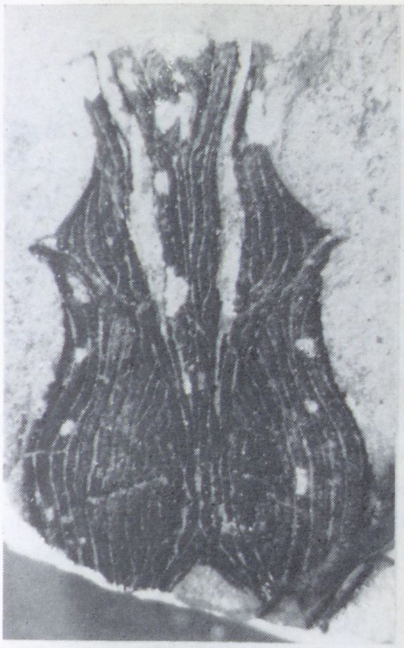
Plate

Figs. 1-3. *Dialipina markae*. 1 - Anterior skull roof; Pi 1383. x 8. 2 - Posterior skull roof; Pi 1384. x 8. 3 - Scale of dorsal or ventral abdominal or caudal region; Pi 1384a. x 10. Lower member of Kureika Formation, Lochkovian, D1; Sida River, Kotui Basin, Siberia. Fig.4. ? *Dialipina*, left cleithrum in internal view; Pi 1381. x 4. Lower member of Kureika Formation, Lochkovian, D1; Koldy River, Kotui Basin, Siberia. Scale equals 1 mm.

Plate



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The actinopterygian *Cheirolepis* from the Devonian of Red Hill, Nevada, and its implications for acanthodian - actinopterygian relationships

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Abstract. The Red Hill actinopterygian *Cheirolepis* is described. Among representatives of this genus, the Red Hill specimen is closest to *Cheirolepis canadensis*, thus allying the Red Hill fauna even more closely with that of Scaumenac Bay. The remains are also notable for the presence of unjointed fin- spines, which suggests a closer relationship between the Actinopterygii and the Acanthodii than might have been previously suggested.

Introduction

General remarks on the geography, geology, and paleontology of the Red Hill fish fauna have been published by Murphy, Morgan and Dineley (1976), and by Gregory, Morgan and Reed (1977). The fish fauna is broadly comparable to that of the Old Red Sandstone facies of Europe; it includes dipnoans (Reed, 1985), acanthodians (Reed, 1986), arthrodires, antiarchs, and crossopterygians, in addition to the actinopterygian described here.

The fossils are found concentrated within lime-mudstones deposited in a marine environment. Their age is near the Middle - Upper Devonian boundary.

The specimens were prepared with formic acid and treated with Glyptal. They are kept in the Museum of Paleontology of the University of California (UCMP). The prefix SMNH stands for the Swedish Museum of Natural History.

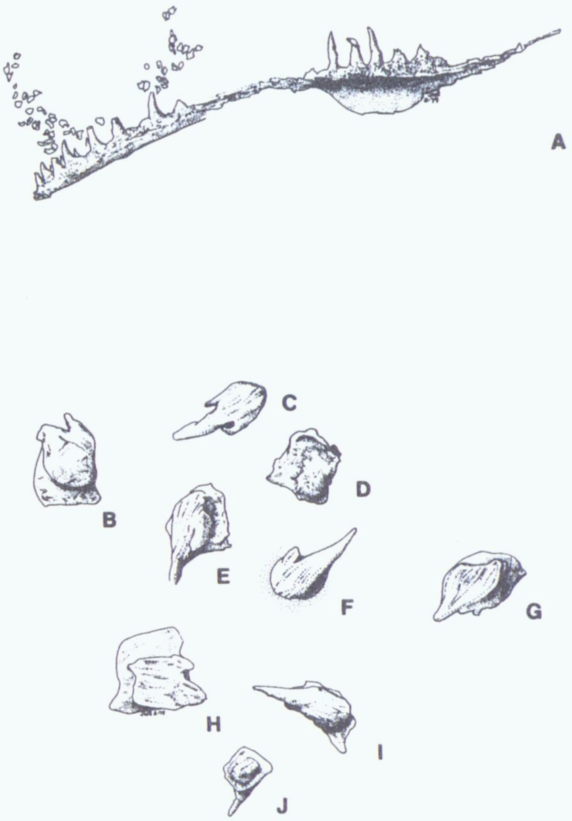
Class Osteichthyes
Subclass Actinopterygii
Suborder Palaeoniscoidea
Family Cheirolepidae
Genus *Cheirolepis*
Cheirolepis* cf. *canadensis

Material. UCMP 123137, lower jaw (Pl., fig.1); UCMP 118287, skeleton fragments, including spines and scales (Pl., fig. 2; Text-figs. 1A-J; 2A,C-E); UCMP 123150, jaw fragment (Text-fig. 2B).

Description. One partially disarticulated skeleton and two isolated jaw fragments are described. In the skeleton, about three or four elongated dermal bones are visible. They are smooth on the inside; externally they are ornamented with a series of narrow, parallel ridges. The ridges are usually continuous, but may be either interrupted or anastomosing in places. On one of the bones the ridges bear small flat-topped tubercles.

Among the bones forming the skeleton, there is a relatively large fragment of one of the jawbones. Seen laterally, its outline is sinuous, suggesting it may be a maxilla. The medial edge of the bone is sharp and overhanging. The inner surface of the bone is smooth. To the left, in Text-fig. 1A (what may be the anterior part of the bone), the overhanging medial edge is less distinct; instead of a rather large concavity beneath the edge, there is a prominent swelling, or ridge present.

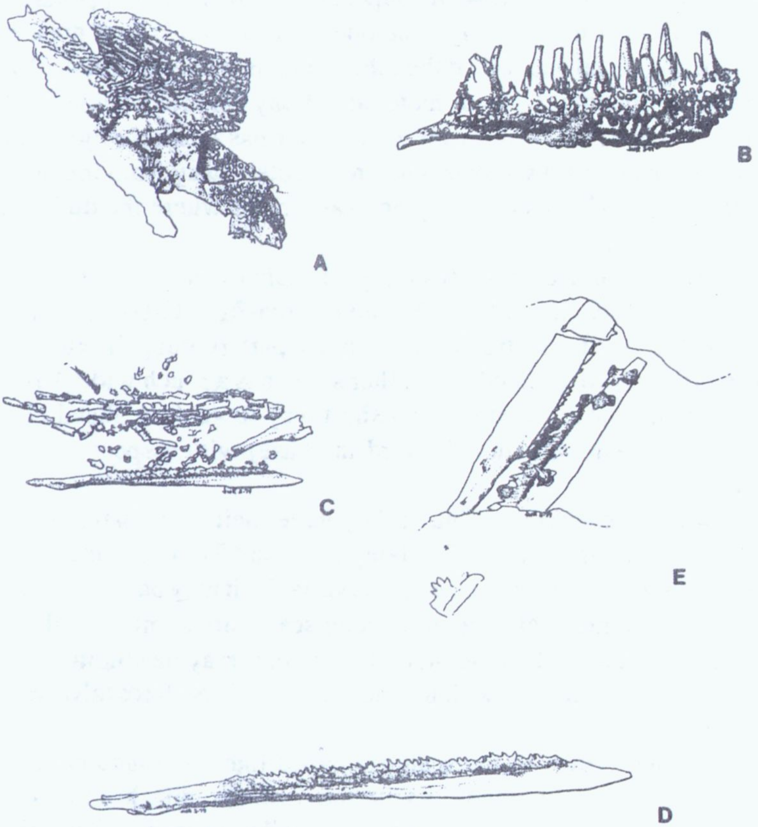
Two rows of teeth are present; a lateral row of small, but very narrow and sharp teeth, and an inner row with much larger teeth. The large teeth increase in size posteriorly, and are slightly recurved posteromedially. They are also very tall and sharp. A faint ridge exists on the anterior edge of each tooth. Otherwise the teeth



Text-fig. 1. *Cheirolepis* cf. *canadensis*. UCMP 118287. A - jaw fragment, medial view, x 3; B, C - scales, external surface, x 25; D - scale, internal surface, x 25; E-I - scales, external surface, x 25. J - scale, internal surface, x 12.

appear to be smooth. A large pulp cavity is clearly visible in the broken teeth. The teeth are fused with the slanting superficial surface of the jawbone; the point of fusion being marked by a faint ring. Teeth generally alternate with deep sockets, although right at the anterior part of the jawbone there are three teeth in a row (and no intervening socket). The base of the middle tooth is missing, and it may be a leftover from a previous growth stage.

On the two isolated jawbone fragments (UCMP 123137, and UCMP 123150) the external surface of the bone is visible. It is ornamented with a series of short, raised ridges which are covered with shiny material. These large ridges are themselves covered with a series of approximately parallel small ridges. On these specimens, the teeth of the lateral row sometimes originate below the superficial



Text-fig. 2. *Cheirolepis* cf. *canadensis*. A - bone fragments, UCMP 118287, x 3; B - jaw fragment, lateral view, UCMP 123150, x 6; C - fin rays and unjointed fin spine, UCMP 118287, x 3; D - unjointed fin spine, UCNP 118287, x 6; E - unjointed fin spines (another occurrence), UCMP 118287, x 6.

margin of the jawbone. Both tooth rows display teeth which are exceedingly tall and narrow.

Part of a fin is preserved (UCMP 118287). It is composed of about ten fin rays. The latter are all jointed. Details of these rays are difficult to distinguish, but on a few of them there is a light grey lustrous surface present on one side, which is ornamented with ridges. There is also a tall ridge running along the flat face of each segment. Several of the segments have, along one edge, tiny teeth which are strongly recurved.

Among the remains of the disarticulated skeleton are unjointed spines with denticulated edges. I interpret them as unjointed fin spines; in each case they are found adjacent and nearly parallel with segmented fin rays. Furthermore, the small teeth on their edges strongly resemble the teeth present on some of the segmented fin rays.

The spines are long and narrow, and taper at both ends. They appears to be wider anteroposteriorly than transversely. The one spine which is best preserved has a gradually tapering distal end, but at the other end it is wide and blunt. These spines are formed of two distinct types of material: a bony smooth portion, dull white in color, and an attached part, forming the teeth, which has a lustrous light grey surface. The teeth occur in at least two rows, and are directed away from the proximal end of the spine. The distal ends of the spine bear a ridge where the dull colored part meets the lustrous part.

There are two unjointed fin spines lying adjacent to one another (Text-fig. 2E). One of them resembles the isolated fin spine (Text-fig. 2C-D), except that a fine ribbing is visible on the lustrous denticulated part running in about the same direction as the teeth are pointed. The other spine has a much wider basal portion. On it, the teeth appear to extend only a short way toward the distal end, and are pointed in the opposite direction (toward the base) with respect to those on the opposite spine.

The scales are exceedingly minute; they have their own distinctive structure, which includes: 1) a narrow neck, 2) a bony base, and 3) a complicated superficial ornamented crown. The outline of the base is variable; it may be square, rhomboidal, nearly circular, or somewhat irregular. Many scales are symmetrical; one corner protrudes farther laterally than the other. One corner may be slightly rounded. On the base is found the basal boss, which varies in height. It is almost always elongated and situated off center.

The ornamented crown of the scale is shaped like a cornucopia. It is usually contracted basally where it blends in with the neck that attaches to the base. It is widest anteriorly and it is drawn out onto a long tail posteriorly. This tail is usually more or less straight but is sometimes twisted to one side. Accessory tails, or wings (or spines) may be present on each side of the tail. If present, the wings are usually very short. The superficial surface of the scale is ornamented with between four and eight ridges; anteriorly they are directed slightly laterally, but they converge posteriorly. The scale resembles a wing in that the place of maximum thickness is situated about one third of the way back from the anterior edge.

Comparison. In their detailed redescription of the species of *Cheirolepis*, Pearson and Westoll (1979) were able to point out a number of character states which differentiated the Middle Devonian *C. trailli* from the Upper Devonian *C. canadensis*. Among these are two sets of features which can also be applied to the comparison of the described Nevada material: the condition of the dermal bone ornamentation, and the morphology of the scale crowns. In *C. trailli* the ornamentation is developed as rows of pits, whereas in *C. canadensis* it is developed as rows of ridges. From what little can be seen of the dermal bone ornamentation in the Nevada specimens, it more resembles the condition in *C. canadensis*.

Comparison of the scale crown morphology is more difficult; there is apparently some variation that depends on the position of the scale on the body of the animal, and no detailed study of this, similar to what Märss (1982) accomplished for *Thelodus* has been done. But it nevertheless appears that *C. trailli* has scales on which the spines of the crown are both more numerous and longer than those found in *C. canadensis*. The scales of *C. canadensis* are virtually indistinguishable from those of the Nevada specimens. The overall shape of the crown is the same in the two forms; one spine drawn out into a long tail is usually present, although sometimes absent (as drawn in Lehman, 1947). This detail is easily obscured by matrix and is vulnerable to destruction during preparation (Pearson and Westoll, 1979). The number of ridges ornamenting the crown is about the same, as is their direction. Lateral spines, or accessory wings, are not common, but are sometimes observed. The tail is usually straight, but is sometimes bent, as drawn by Gross (1947, Text-fig. 25B). The only sure difference between the scales of the two forms is that the ones from Nevada are white, and the ones from Canada are black.

By contrast, in *C. trailli*, the spines of the scales are generally or supposedly longer and more numerous. It may also be noted that the outline of the crown, as seen superficially, is more nearly circular; the spines being of more nearly equal length (no single spine being longer or drawn-out into a tail). In addition, many scales on a specimen of *C. trailli* from Edderton (SMNH P.4266) have more numerous ridges (13-17). However, there are other scales present in the specimen, though vastly fewer in number, which look more like *C. canadensis* scales: they are elongate, have a long posteriorly projecting tail, and may even have fewer (about six) ridges. This specimen indicates how uncertain isolated scales are for the taxonomy of *Cheirolepis*. Again, variations according to position have yet to be determined.

Both *Cheirolepis gaugeri* and *C. gracilis* are known only from scales (Gross, 1973, Pls. 35-36). Pearson and Westoll (1979) chose to regard them as incertae sedis. In *C. gaugeri* the scales are very similar to those of both Nevada specimen and *C. canadensis*. The chief differences are that the posteriorly projecting tail is very short in *C. gaugeri*, and the accessory wings are more common and more prominent. The scales of *C. gracilis* resemble those of *C. graugeri* in the relatively strong development of the accessory wings. These scales have, it appears, more than one level of ornament. They also have a large number of ridges (up to 28).

Unjointed fin spines may also exist in *C. trailli* and *C. canadensis*. There is a specimen of *C. trailli* (SMNH P. 4266) where some sort of unjointed spine is lying among partially disarticulated scales; what the spine is and what it belongs to remains uncertain. In *C. canadensis*, there are fin rays near the anterior edge of the dorsal fin which may be unjointed. The Canadian material is known from split slabs, and the material is cracked and tends to be obscured by matrix. There may be small teeth present on certain rays. The elongated fulcral scales on the leading edge of the caudal fin are unjointed. These scales are also significantly longer than the drawing published by Lehman (1947, Text-fig. 17) indicates. Some of the fin rays have ornamented exteriors. This ornamented surface is shiny and black, and probably corresponds to that part of the unjointed spines of the Nevada material which is shiny, light gray and denticulated.

On the whole, the Nevada material very strongly resembles the Canadian material; enough, on the basis of the fragmentary remains, to suggest an identification to the level of *Cheirolepis* cf. *canadensis*.

Remarks. Pearson and Westoll (1979) and Pearson (1982) summarized the changing history of the views on the affinities of *Cheirolepis*. Although now regarded as a palaeonisciform, some of the earlier authors entertained conjecture of acanthodian affinities. The present study does not affect these opinions, but it does have significance to the question of the relationship of the acanthodians to the Osteichthyes. According to Pearson (1982, p. 60) it is the current "minority opinion" that the acanthodians are directly ancestral to the Osteichthyes, a view held by Heyler (1958, 1962) and Schaeffer (1968). It was also noted by Pearson (1982, p. 61) that "There are two major objections to the acanthodians as osteichthyan ancestors: their spinous precaudal fins and their lack of dentigerous dermal bones around the jaw and gill apparatus". The existence, in *Cheirolepis* cf. *canadensis*, of unjointed fin spines may remove one of these objections.

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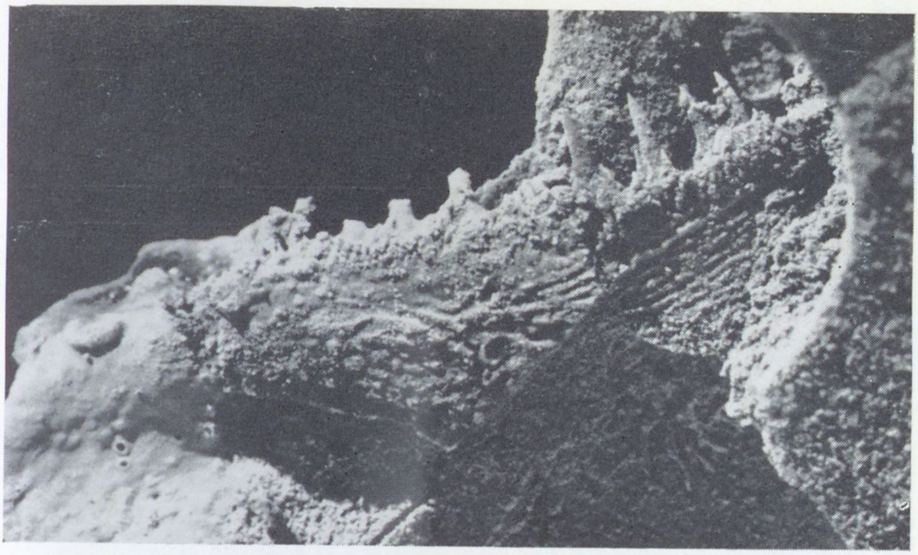
Plate
Cheirolepis cf. *canadensis*.
Fig. 1. Jaw, labial view. UCMP 123137, x 9.
Fig. 2. Skeleton fragment. UCMP 118287, approx x 2.

Plate



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Depositional environment and burial conditions of fish remains in Baltic Middle Devonian

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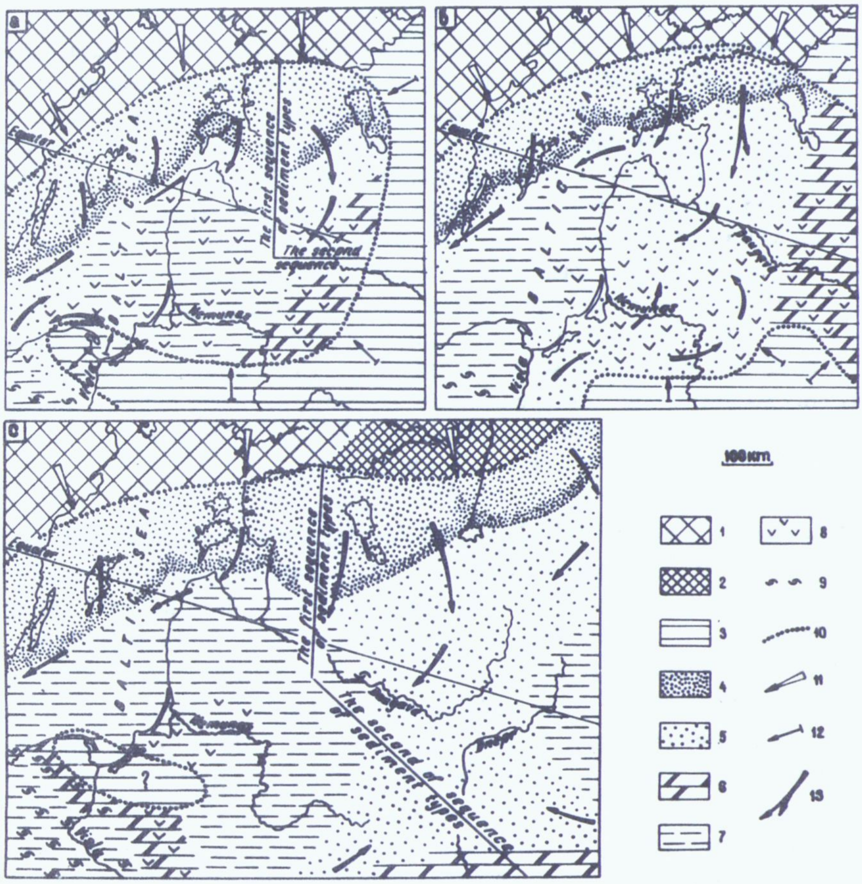
Abstract. Two sequences of the sedimentary facies of the Middle Devonian and early Late Devonian basins are established. The first sequence proceeds from the basic source area of clastic material in the north where marine shallow-water and subaqueous- deltaic, mostly sandy sediments accumulated, to the south towards the central part of the basin predominated by clayey-silty muds. Rather thoroughly have been described slump depressions on submarine delta slopes filled with fine-dispersed clays containing rich burials of well-preserved organic remains, particularly articulated fishes. The second sequence of sediment types spreads in the eastern marginal zone of basins adjacent to peneplained land characterized by the Lower Palaeozoic carbonate rocks. Clayey-dolomitic muds occurring there accumulated in the shallowest saline part of the basins. Westwards the role of sandy deposits increased, but still farther towards the central part of the basins clayey-silty sediments started to predominate. Dynamic, oxidizing-reducing and salinity regime of sediment accumulation, characteristics of the distribution of organic remains and reasons of their variable preservation have been presented.

The genesis of sediments of the Baltic Middle Devonian transgression maximum phase represented by domerites, dolomites, carbonate siltstones and clays of the Narva Regional Stage, has been thoroughly studied and does not give reason for discussions. Sedimentation took place in saline shallow-water marine basins. Less definite is the genesis of terrigenous units belonging to the initial and the final stages of the Middle Devonian and the early Late Devonian. At present the conclusions concerning the dynamic environment of sedimentation do not cause any doubts. For different stages of the Early, Middle and the beginning of the Late Devonian the stream direction pattern was, in general, identical. The direction of the current was from the north to the south, from the central part of the Euroamerican Devonian continent to the inner basins of its marginal zones (Text-fig.1). A similar hydrodynamic environment prevailed in other marginal zones of that continent: Severnaya Zemlya, North Timan, Scotland, Appalachians, Arctic Canada, etc.

At present, such depositional environments are widespread on the alluvial plain; in the seas alongshore currents prevail. Therefore the concept of Devonian sandstone formations as typical ancient alluvium used to be quite popular and is still recognized by some scientists. Still, direct comparison of hydrodynamic conditions in ancient and modern basins is not correct since in different areas there are examples of thoroughly studied ancient basins characterized by the direction of bottom currents (and, consequently, sediment transport) from basin margins towards their central parts, from thinner and coarse-grained sediment layers to thicker and more fine-grained ones. This fact has been established by mass

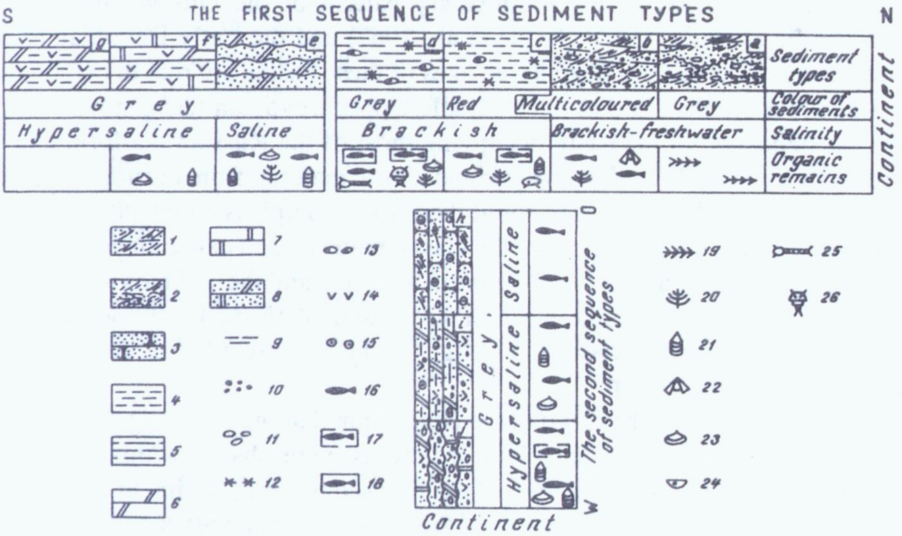


Text-fig. 1. Early-Middle Devonian sedimentary basins of Baltic area. a - Dittonian, b - early Eifelian, c - Givetian/ early Frasnian. 1-3 - dominate denudation area (1 - supplied fresh unweathered clastics, 2 - supplied chemically weathered clastics, 3 - supplied a few unweathered clastics from flatland built of the Upper Palaeozoic carbonate rocks); 4-8 - dominate accumulation area (4 - marine deltaic clastic sediments, 5 - shallow-marine clastic sediments, 6 - shallow-marine marls and clays, 7 - relatively deep-water clastic sediments, dominantly silts and clays, 8 - gypsinate sediments); 9 - marine invertebrates; 10 - denudation and accumulation area margin; 11- 12 - clastics supply direction (11 - dominate, 12 - unimportant); 13 - palaeocurrent directions in sedimentary basins.

measurements of oriented structures. Marine genesis of several such standard basins has been established by the presence of typical marine invertebrate fossils (Pettijohn, 1975; Verzilin, 1979; Grossgeim et al., 1984). So, sand layers deposited by fast water currents can be both continental and marine ones.

Sandy sediments prevail in the northern part of the basin near the foot of collapsing mountain ridges (Text-fig. 1). To the south, currents were decaying: in the central and the southern parts of basins clayey/sandy sediments were widespread. Clays were deposited in local bottom deeps. In connection with that there has been established usual for sedimentary basins (perpendicular to the palaeoslope) sequence of sediment types. Near the source area in the proximal part of this sequence the coarse-grained material deposited, but fine-grained sediments deposited towards the inner part of the basin in the direction of the distal part of the sequence (Text-fig. 2).

During basin development stages when in the eastern part there was peneplained lowland, formed by lower Palaeozoic carbonate rocks, in the eastern nearshore zone of the basins unattainable for the main clastic material flow from the Baltic Shield,



Text-fig. 2. Sequences of sediment types and organic remain distribution. 1 - cross-bedded sand; 2 - cross-bedded sand with slump structures; 3 - dolomitic sand; 4 - silt; 5 - clay; 6 - domerite; 7 - dolomite; 8 - domerite and psammitic dolomite; 9 - silty sediments; 10 - quartz pebbles; 11 - silt and clay pebbles; 12 - ferruginous nodules; 13 - phosphatic pebbles; 14 - gypsinate sediments; 15 - ball-shaped nodules with carbonate cement; 16 - fish bones; 17 - fish remains: complete specimens without caudal part; 18 - fish remains: articulated specimens; 19 - silicified wood *Nematophyton*; 20 - plant macrofossils in general; 21 - inarticulate brachiopods; 22 - articulate brachiopods; 23 - conchostracans; 24 - ostracodes; 25 - mysidians; 26 - merostomes.

the deposition of clayey-dolomitic sediments, silts and sands took place making up the second sequence of sediment types.

The distribution of sediment types has changed markedly depending on different age of the basins. At the beginning of the Eifelian transgression (Text-fig. 1b) the sea basin, as compared to the Early Devonian ones, has prograded as a result of subsidence of the Moscow syneclise. The shallow-water sands and silts developed considerably, but relatively deep-water silty sediments degraded and occupied only the axial part of the Polish - Lithuanian syneclise. At the same time, to the east of the Vilaka arch small amounts of clastic material entered the adjacent Moscow syneclise, where mainly gypsinate clayey-dolomite silts with some sand material were deposited, characterizing the proximal zone of the second sequence of sediment types.

Certain similarity with the second sequence of sediment types can be observed in Narva basin during the Middle Devonian transgression maximum. The purest carbonate sediments have deposited at that time on the elevated Belorussian-Mazur anticline area. At the more intensely subsiding central and western parts of the basin considerable admixture of the terrigenous component in the clayey-carbonate sediments took place (Valiukevičius, et al., 1981). The second sequence of sediment types bears similarity to the sedimentary pattern of the Ordovician - Silurian Palaeobaltic (Männil, 1966; Gailite et al., 1967) and the Early Devonian (Kuršs, 1986) basins. The eastern nearshore zones of these basins are rich in carbonate.

Usually more than 200 m thick Middle/Upper Devonian terrigenous sediment unit has deposited in the basin occupying most of the Russian platform and was formed by a strong flow of freshwater and clastic material from the northern source area. During the formation of this unit there were no uplifts on the platform which could slow down the main flow of the clastic material and cause clayey-carbonate sedimentation. Such uplifts, the Voronezh anticline and the Tokmov arc existed in the Givetian only in the southern part of the Russian platform. On the northern slope of the uplifts mentioned above (Text-fig. 1c) the accumulation of domerites took place (Tikhomirov, 1967).

Lithological studies have led to the conclusion that the coarse- grained alluvial fan and sandy-clayey alluvial plain sediments were absent within units under consideration. In the proximal end of the first sequence of sediment types marine deltaic sands are situated. As a result of Pre-Quaternary denudation they have been preserved only in the north-eastern area where washout products of the chemical crust of weathering entered the Devonian basins. It has greatly influenced both the sediment composition and the preservation of organic remains. So, the removal of iron compounds from the crust of weathering has caused the light colour of sediments, while the chemical weathering of the parent rocks has determined high content of stable components of the mineral association (quartz, zircon, tourmaline, kaolinite, etc.). In marine deltaic sands authigenic forms of silica are abundant: the rims of feldspar and quartz grain regeneration, flint concretions with invertebrate marine fauna (stromatoporoids, articulate brachiopods, rugose corals) and silicified wood of *Nematophyton.* Fish remains are absent in light mature marine deltaic sands, but there is no doubt that the deltaic area was densely populated by fish. These silica rich sediments, probably, are not favourable for the preservation of phosphatic fish bones. Finds of decomposed fish bones and, sometimes, crossopterygian scale imprints whose phosphate core has been completely leached, are a proof of that.

The dynamic environment of marine deltaic sand accumulation was characterized by unidirectional water currents perpendicular to the shoreline; they transported the clastic material in the form of sand waves which deposited in 15-30 cm thick cross-bedded layers. The abundance of sand material, considerable deposition rate (60-80 cm daily) and high-gradient slope of the bottom have led to gravity slidings where one, two or three cross-bedded series were involved and often forming up to 60 m thick slump depressions filled with brecciated material, and in the central part of depressions with dispersed clays.

Deposition of shallow-marine sands (Text-fig. 2b) was abundant on a vast territory at the beginning of the Middle Devonian and during the formation of the Middle-Late Devonian terrigenous unit. They differ from marine deltaic sediments in their variegated and reddish colouring, and less mature mineral association: shallow-marine sands contain somewhat more feldspar, garnet and apatite. The reason is the increase in clastic material from more elevated blocks of the source area (where chemical weathering was absent). Sands of this type are common in the central and the western parts of the basin. Therefore the hydrochemical environment in basins and sediments has not caused the decomposition of fish bones; the situation was favourable for the formation of phosphorite nodules. In one case the occurrence of articulate brachiopods in fine-grained sand of this type has been noticed.

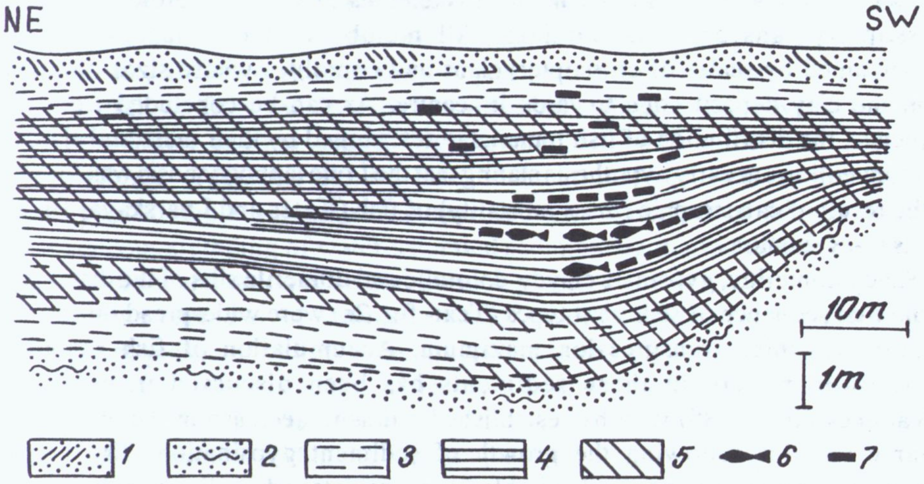
The transport and deposition of sandy sediments usually took place in the form of crescent-shaped sand waves. Oxygen-rich waters and high current speed led to fast decomposition of fish cadavers, fish bone disintegration and rounding, their secondary concentration in cross-bedded sands and conglomerate lenses.

Flat bones (e.g. armour plates and their fragments are situated in parallel to cross-bedding, their dip angle is 15- 20° towards water current and sand wave movement. Flat fish remains like any coarse-grained material of such a configuration moving downwards from the top of sand waves, in most cases did not reach the foot but were stopped in the middle part of the leeward slope of waves. Orbicular bones reached the foot of the wave and, together with rolled pebbles, occurred at the foundation of the cross-bedded layers. When the flow velocity grew, the sand-wave regime of the drift movement was disturbed, the deposition of sand particles was interrupted, coarse-grained material accumulated in the form of short lenses or layers of intraformational conglomerates of inconstant thickness. Sometimes the concentrations of fish remains were considerable, and fish-bone beds developed.

The weakening of the water layer dynamic activity has led to the accumulation of red silts. They are well developed in the relatively deepwater part of the basin and as the slump depression fillings in the marine deltaic sands. Silts are characterized by massive or approximately horizontal bedding referring to calm deposition environment. Small-scale cross- bedding, formed by slow currents, occurs less often. On the bottom of the basin and in the sediments the water was oxygen- rich. Reducing conditions occurred in some places around fish and plant remains. It can be presumed that the rate of silt deposition (as well as that of other Devonian basin sediments) was high: several metres (?) per year which led to quick burial and good preservation of organic remains. Fish remains in siltstones are represented by separate current-sorted, sometimes abundant accumulations; in the Lode clay quarry such silty sediments contain, on some levels, rich accumulations of antiarchs and crossopterygians which are similar to bone beds observed in other areas. The formation of such accumulations in that area was favoured by the presence of slump depressions on submarine delta slopes; the depressions were densely populated by fish which, in turn, was determined by the abundance of their possible food resources, small invertebrates conchostracans and mysidians.

In slump depressions grey dispersed clays were deposited representing an outstanding type of sediments of great lithological and palaeontological significance (Text-fig. 2d). The hydrodynamic deposition conditions of these clayey sediments were characterized by little water mobility: oriented structures do not occur there. Some orientation of fish cadavers in the well-known Lode taphocoenosis is a result of the existence of weak currents. The stagnation of bottom waters has led to the formation of reducing conditions on the bottom and in the sediments and to the occurrence of well-preserved organic remains in clays. One more factor, contributing to the outstanding preservation degree of organic remains in those clays, was considerable deposition rate estimated by studying rhythmic sections of clays. It is assumed that marked rhythms observed in the Lode quarry are controlled by the seasonal rainfall at the clastic material source area. During the formation of the lower part of the grey clay unit, the deposition rate was 20 cm/yr and more, judging by sediments consolidated in postsedimentation processes. The deposition rate subsequently lowered to 5 cm/yr and less.

Due to mentioned favourable factors fine-grained dispersed clayey sediments are unique from the point view of the abundance and the degree of preservation of organic remains including fish. When mining in the Lode quarry (upper part of the Middle-Late Devonian terrigenous unit) three occurrences of articulated fish specimens were recorded. During the excavations in 1971, the results of which have been published (Lyarskaya and Mark-Kurik, 1972; Kuršs and Lyarskaya, 1973), in the 10 m long layer bordered by dislocations on every side, in the upper part of rhythms with the maximum clay content several hundreds of complete individuals of placoderm fish *Asterolepis ornata* and crossopterygians *Laccognathus panderi* and *Panderichthys rhombolepis* were obtained. Separate fish bones and skeleton fragments were almost always absent. Together with fish bodies there occurred



Text-fig. 3. Distribution of fish remains in a lens of grey dispersed clay. Lode quarry, Latvia. 1 - cross-bedded sandstones; 2 - ripple-bedded sandstones; 3 - siltstones; 4 - clays; 5 - red coloured rocks; 6-7 - fish remains (6 - articulated specimens, 7 - bones).

phosphorite nodules with fragments of fish bones and conchostracans. In the basal silty part of the rhythms on bedding planes there was a continuous layer of well-preserved plant remains.

The excavations of 1976 were the most informative considering the burial conditions of fish remains because bone-bearing layers could be followed at the distance of 120 m. Articulated fish skeletons are confined to the areas of the maximum thickness of the clay layer characterized by greenish-grey colour and considerable dispersity (Text-fig. 3). In those areas, probably corresponding to basin bottom deeps, fish cadavers accumulated as a result of sorting of organic remains by weak currents. Along the borders of the bottom deeps in somewhat elevated bottom areas a great number of separate bones accumulated, but in areas with still smaller depth the number of bones decreased quickly. The colour of clays changed from greenish-grey to variegated and, further, to red.

Such sorting of organic remains was observed during the excavations of 1989 in another lens of grey dispersed clays filling a clearly defined slump depression. The results of studies on the burial of fish are summarized in the paper by I. Upeniece and J. Upenieks in this book. As can be concluded from this material, the fish remains are more varied than in the earlier studied burials. Therefore, the distribution of different remains from the edge of the depression towards the central part of the clay deposit, i.e. towards the deepening of the sedimentation basin, is more complicated. The succession of remains includes: bones of adult asterolepids and crossopterygians - complete bodies of adult and juvenile asterolepids - armour plates of young asterolepids - articulated skeletons of young asterolepids, small crossopterygians and acanthodians. All members of this succession are accompanied by scales of crossopterygians and coprolites whose sizes diminish from the clay deposit edge towards its centre. As can be concluded from the sequence, the distribution of fish remains is determined by their mass and size. In this convention our early hypothesis stating that the Lode taphocoenosis was formed in the result of catastrophic (mass mortality) of fish (Kuršs and Lyarskaya, 1973), needs re-evaluation.

Sandy domeritic, gypsinate clayey-dolomite and domerite silts of the distal part of the first sequence of sediment types (Text- fig. 2e) were widespread during the Middle Devonian transgression maximum. Accumulation of fish remains' distribution pattern in these sediments has been discussed in detail by J. Valiukevičius (1985) who has established a drastic decrease in the amount of organic remains following the growth of sediment gypsination. The Upper Devonian deposits are the most suitable for more detailed studies of this type of sediments.

Shallow-water marine sediments of the sequence situated near the eastern shore of the basin are represented by dolomitic and clayey-dolomitic silts (Text-fig. 2j) which usually contain admixture of sands. Due to relatively high hydrodynamic activity of the environment as a result of wave and/or current action, structures of mixing and redeposition are often observed in the sediments; sometimes slump structures also occur. Fish remains are abundant but, during mixing and redeposition of sediments bones are usually crushed. In some cases well-preserved parts of fish skeletons have been found. Conditions must have been favourable for fishes. Due to small amount of clastic material entering the eastern part of the basin, water was cleaner there and had relatively stable salinity. Low sedimentation rate has favourably influenced the development of small invertebrates, conchostracans and lingulids, serving as food for some fish groups. This type of sediments is characteristic of the regressive part of the Silurian - Early Devonian sedimentation stage. Under similar conditions during the first half of the Middle Devonian some domerite layers have been formed.

The next type of the second sequence of sediments (Text-fig. 2i) has deposited in less active hydrodynamic conditions and is represented by greenish-grey clayey-dolomitic sediments with lingulids and conchostracans. Mixing and redeposition structures are absent, but the admixture of sandy material is quite characteristic; it is distributed very irregularly in the form of complex streams and "vortices". Carbonate oolites occur rather often as well as pseudoolites, gypsum layers and veins, small quartz pebbles. Fish bones and fragments are abundant and occur together with coarse-grained material. So, these sediments characteristic of calm hydrodynamic environment contain coarse- grained material. The presence of carbonate oolites in sediments is a proof of intensive wave or tidal current activity. Sediments of this type occur in sections of the Middle Devonian transgressive phase. Its deposits include also the next member of the second sequence of facial types: grey massive and small-scale cross-bedded sands with carbonate oolites and pseudoolites. Sediments often contain poorly preserved fish bones, they are represented mainly by poorly rounded fragments.

As follows from the character of different sediment facial types, they are of shallow-water marine origin. Occurrence, although rather rare, of marine invertebrate organisms should also be mentioned, as well as abundance of phosphorite nodules, slump structures and great depressions formed during the subaqueous slumping of water-saturated sediment on marine deltaic slopes where intensive accumulation of sediments took place.

Marine character of sediments under investigation is further confirmed by similar sequence of sediment facial types in the eastern part of the Devonian (see the second sequence of sediments) and the Ordovician-Silurian basins, by constant thickness and structure of stratigraphic units which can be traced for several hundred kilometres within the Russian platform.

Fish remains, as follows from the data collected, occur in sediments deposited in almost all types of the environment. They are absent only in very mature white submarine deltaic sands. Probably, that zone also had abundant fish population but later the bones were dissolved. The concentration of fish remains decreased also at the distal end of the sequence of sediment types in the zone of somewhat more deepwater clayey-carbonate sedimentation. That zone was less densely populated by fish which preferred, due to the availability of food, the most shallow zones of the Devonian seas. Living conditions of these organisms have been negatively influenced by abrupt rise of the salinity of water, which has caused, e.g., almost complete absence of fish remains in gypsinate deposits.

The degree of preservation of fish remains was greatly influenced by the dynamic environment in the basin. Under conditions of high water activity accompanied by oxygen-rich environment, when multicoloured and red sands and silts accumulated, fish cadavers were quickly decomposed, bones were pulled apart and crushed by currents. Secondary accumulations of remains were formed, some of them rather big. The distribution pattern of fish-bone beds in sediments fully depends on the hydrodynamic regime in basins and the inflow of the clastic material.

The decrease in the activity of sedimentation hydrodynamic regime, in general, led to better preservation of fish remains. Sands and silts deposited in slow flows sometimes containing big parts of fish armours. With weakening of streams articulated fishes accumulated in dispersed clays. Recent data have confirmed that burials of this type in the Lode clay quarry are allochthonous and are not due to mass mortality of fish.

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Reconstruction of abiotic and biotic environments in Devonian estuarine-lagoonal basins by using Mesozoic and Cenozoic analogs

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Abstract. There are some connections between the main characters of the structure of the Mesozoic and Early Cenozoic vertebrate assemblages, environmental conditions of organisms and deposition. The observations about the Mesozoic and Cenozoic might be used for the reconstruction of Devonian situations if we consider the structure of Devonian assemblages and information on the structure and texture of Devonian sediments. Several Spitsbergen and Baltic vertebrate localities of the Early and Middle Devonian age formed in estuarine-lagoonal basins, e.g. those of the Wood Bay Series and the Aruküla Formation.

Aquatic vertebrates and lingulid brachiopods have, as a rule, a very important role in the balance of the energy of water ecosystems with some anomalies of abiotic factors (salinity, content of O_2, temperature, currents, etc.). In aquatic ecosystems with normal water salinity the flow of energy from organic detritus and plankton is directed chiefly to invertebrates which are mainly protected by carbonate shells. In environments with normal water salinity vertebrates usually consume only small amounts of available food, as many groups of invertebrates have some advantages in these situations. Therefore, localities with abundant remains of fossil aquatic vertebrates contain very scarce invertebrate fauna while, on the contrary, at sites with diverse invertebrate remains, bones and teeth of vertebrates are usually rare.

With deterioration of the normal environments of aquatic vertebrates, the diversity of these animals decreased. The survived species lived in conditions of weak competition. As a result the size of such a population usually increased. Therefore the largest density of populations of aquatic vertebrates usually associated with a low diversity of species. Diversity of vertebrate groups and abundance of each species in localities of Wood Bay Series of northern Spitsbergen (Lower Devonian) and Aruküla Formation in Leningrad Region (Middle Devonian) suggest that vertebrate localities of these areas formed in environments with constant big changes in abiotic factors.

Interspecific competition is usually low, and biotic situation is not hard in extremely difficult abiotic conditions (as diversity of competitors is not high). Therefore the rate of evolution slows down, but specimens with "side-stepped" morphology and ecology tend to survive, as they can use somewhat different food and other resources than "normal" specimens of this species need. As a result, the changeability of species that lived in such situations increased.

Groups of agnathans and fishes represented in the Devonian do not have recent survivals resembling Devonian forms in morphology and living conditions. If so, we cannot properly use the Devonian vertebrates as indicators of concrete factors of ancient environments.

Many Mesozoic and Early Cenozoic Groups have recent species with stable morphology and, as it seems, ecology. Some of these living fossils are obviously conservative in some of their adaptations, e.g. heterodont and pristioid chondrichthyan fishes, amiids, gars, albuloids, some labroids, xiphioids, some groups of aquatic and semiaquatic amphibians, turtles, snakes, crocodilians, etc. The structure of these assemblages can also be used for the reconstruction of the environment. E.g., the diversity of chondrichthyan fauna depends on water salinity: in the Black Sea with it being 18 per mill or lower only three species, as a rule, are present, while at the same latitude in the Atlantic with the salinity of 34 per mill there are several dozens of species of this group. Another example: crocodiles, as water animals, live in the environments with the average air temperature of January exceeding 10-15°C. If so, we may use ancient representatives of recent groups as, at least, approximate indicators for the reconstructions of Early Cenozoic and Mesozoic environments and for some sedimentary conditions of these ages. The studies carried out enabled to find some connections between the main features of the structure of the Mesozoic and Early Cenozoic vertebrate assemblages, the environmental conditions of organisms as well as deposition. Similar observations about the Mesozoic and Cenozoic might be used for the reconstruction of Devonian situations if we consider the structure of Devonian assemblages and information on the structure and texture of Devonian rocks. This work carried out in 1968-1989 has shown that localities with vertebrate remains in Kapp Kjeldsen, Keltiefjellet and Stjørdalen Formations of Wood Bay Series of Haakon VII and Andrée Lands and in the Aruküla Formation in the Oredezh and Lemovzha Rivers region formed in estuarine-lagoonal basins with many bars, spits, peninsulas and islands (represented by mosaic pattern of water and land). Water was more or less muddy, brackish, with changing salinity, containing large amounts of organic detritus produced near the coast of basins or moved to the area by fresh-water streams from coastal plains. Such ecosystems were unique, obviously differing from marine and fresh-water ones (see Odum, 1975).

Rich channel-lag and channel-fill localities of disarticulated and partly associated skeletal remains of brackish- and fresh- water vertebrates in the Neogene, Paleogene, Cretaceous, Jurassic, Permian, and Devonian formed mainly not in fluvial channels, as reconstructed for Miocene and Permian examples by Behrensmeyer (1988), but in deep channels that connected shallow lake-like estuarine-lagoonal and fresh-water basins.

Alternate currents were caused in such channels by the differences in atmospheric pressure and by the winds of various directions. Recent hydrological models can be seen in the southern part of Lake Khanka (Far East of Russia), also in adjacent lakes connected with Khanka by channels. Deep parts of these ancient channels worked as pitfalls for skeletons and disarticulated remains of vertebrates that were moved by two-way currents. Localities in mentioned ancient areas were formed on the channel bottom eroded by strong alternate currents (e.g., channel-lag facies in Shatyrtau locality of Santonian-Early Campanian dinosaur remains in Central Kizylkum Desert), in abandoned channel (as in Middle Devonian locality of microvertebrate remains in channel-fill facies near Belogorka, the Oredezh River, Leningrad Region) or near two mouths of a channel (channel-throw facies in Coniacian of Dzhyrakuduk in Kizylkum). Channel-lag deposits of investigated localities usually occur in outcrops as lower parts of chutes with sands, mud-clast conglomerates and abraded vertebrate remains; channel- fill deposits are represented in middle and upper parts of symmetrical lenses of more fine-grained sediments with vertebrate materials of better preservation. Channel-throw deposits look as sandy or gravel layers (or thin lens, or a series of layers or lenses) of usually unbedded or poorly bedded sediments with unsorted and usually disarticulated vertebrate remains, with long and flat bones arranged horizontally.

If large, brackish-water basins have estuarine type of circulation (Schopf, 1982) caused by humid or semihumid balance of precipitation, then carbonate pebbles, otoliths of fishes, carbonate shells of invertebrates and sometimes soft tissues of animals and many other remains are phosphatized, and phosphate coprolites of predators are not dissolved. In this situation upwelling currents of water (with O_2 deficiency) that moved from the depth of the sea were the sources of PO_4 -ion for the estuarine ecosystem. Large amounts of biogenes caused high productivity of organic matter in the basin, the prevailing of Fe^2 ion over Fe^3 in sediments and abundant grey, green and blue colours of deposits.

Red colour of sediments in basins is usually caused by downwelling currents in lagoons (Mediterranean type of water circulation) in situations of arid and semiarid climates when water masses with low amounts of biogenes, high quantity of O_2, increased salinity and gravity moved from the surface to the bottom of lagoons (therefore Fe^3 ion prevail over Fe^2 in sediments) and further into the depth of the ocean. This flow of the water and warmth might have heated deep water of the ocean up to the creation of warm ocean upwellings at higher latitudes and to the rebuilding of the climate of the whole planet (in Early and partly in Middle Devonian, in Late Permian, in Late Jurassic - late Cretaceous, in Late Paleocene - Eocene and possibly in Early Oligocene).

Anoxic events in the ocean with the suppression of deep water and vertical currents or nondeposition of sediments in the situation with strong deep water currents and also important simultaneous extinction of many marine, estuarine-lagoonal and terrestrial groups of organisms might have been caused at times by changes from one type of circulation in the ocean to another.

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The latest Devonian, Khovanian vertebrate assemblage of Andreyevka-2 locality, Tula Region, Russia

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Abstract. The vertebrate assemblage from Andreyevka-2 locality is described (Upper Famennian, Khovanshshina Beds of the Zavolzkh Formation, Tula Region). Burial took place in the continental basin of the estuarine type with unstable salinity causing impoverishment of the vertebrate and plant assemblage (blue-green algae, charophytes, ostracodes, worms and bivalves). The biocoenosis was a self-providing detritus-feeding system. The vertebrate assemblage includes the antiarch *Remigolepis armata* Lukševičs, crossopterygians *Eusthenodon* sp. n., *Chrysolepis* sp. n. and *Strunius* sp., the dipnoan *Andreyevichthys epitomus* Krupina, Chondrichthyes fam., gen. et sp. nov. and the tetrapod *Tulerpeton curtum* Lebedev. Its comparison with the East Greenland assemblage of vertebrates including tetrapods is given, their considerable structural similarities are brought out and the exclusively aquatic mode of life of the tetrapods *Ichthyostega* and *Tulerpeton* inhabiting the two basins is shown.

Introduction

A new Late Devonian vertebrate locality, Andreyevka-2, was discovered during a field trip in Tula Region (Suvorov precincts) in the central part of Russia, about 200 km from Moscow.

The site lies on the bank of the small Tresna River, about 300 m upstream from Andreyevka village. The fossiliferous limestones are strongly inclined in the direction of the slope due to a karst gap or a landslide. The total amount of samples collected is estimated at about 1.5 tons. Up to now only one tenth has been dissolved and sorted.

The amount of bones and scales is about ten thousand; they are mostly detached, but sometimes articulated. The chemical preparation gave a possibility to extract the entire mass of bones included in rock samples, which made it possible to exclude the biased sampling.

In order to define the position of the assemblage described below, first the section of the locality should be discussed briefly (see also Lebedev, 1986). The lowermost bed is a limestone layer containing separate bones and scales of *Holoptychius* cf. *nobilissimus* Ag. and *Chrysolepis orlensis* Lebedev. It is overlain by an almost continuous stromatolite layer and, further up, by limestone with undetached *Remigolepis* carapaces and separate bones of dipnoans and crossopterygians. The incomplete skeleton of *Tulerpeton curtum* was discovered in this very layer. The overlying layer, about 10 cm thick, is a bonebed abounding in bones, scales and teeth of the antiarch *Remigolepis armata* Lukševics, crossopterygians *Eusthenodon* sp. n., *Chrysolepis* sp. n. and *Strunius* sp., the dipnoan *Andreyevichthys epitomus* Krupina and Chondrichthyes fam., gen. et sp. n. The upper part of the section shows limestone and clay in alternation, containing a few detached scales and bones of fishes.

The precise dating of the locality is based on ostracodes (assemblage *Carboprimitia turgenevi - Tchizhovaella primula - Maternella hemisphaerica*) indicating the uppermost Famennian age (Fa 2d-Tn 1a of the Franco-Belgian Basin). Well- reserved ostracodes are abundant. Shells of indeterminable very thin-walled bivalves and the gyragonites as well as the stem churn-staffs of the charophyte algae *Quasiumbella* are rare. The shells of the sedentary worms *Serpula vipera* Venyukov are plentiful on the upper surface of stromatolites or penetrating it.

The vertebrate-bearing unit can be easily correlated at the generic level with the *Remigolepis* Group of East Greenland; two genera are common: *Eusthenodon* (not found elsewhere in the world) and *Remigolepis*, known also from Scotland, Australia and Ningxia Province of China (Jarvik, 1952, 1985; Stensiö, 1931: Andrews, 1978; Campbell, Bell, 1977; P'an, 1981).

One of the most serious problems in reconstructing the fossil assemblage is correct identification of the burial type: it may be either autochthonous or allochthonous. In our case the problem may be solved if we take into account the absence of the powerful water-flow into the basin which is proved by an almost complete absence of coarse-grained material: the limestones contain a lot of clay particles and a very small amount of fine-grained quartz sand. The bones are sorted neither according to their size nor their form and are lacking any orientation. Some bones (e.g. the fragment of *Eusthenodon* sp. n. squamation, PIN no 2921/15) are articulated, showing almost complete maceration. The transportation of cadavers was rare or missing. The state of preservation of the bones is perfect. All these facts allow to consider the taphonomic assemblage as a biological community.

The presence of stromatolites indicates either hypersalinity or hyposalinity of water in the basin (Makhlaev, 1966; Krylov, 1975). The absence of evaporates, although strongly witnessing in favour of it, does not fully prove the hyposalinity hypothesis. To keep both hyposalinity and water level constant, so that it would equal evaporation, there must have existed a strong fresh- water flow from the continent; that should inevitably bring along coarse-grained terrigenous material of which there is actually none. Also a complete absence of the remains of terrestrial plants or even the plant detritus in the basin seems to be characteristic of this period.

This disputable evidence can possibly be explained by significant fluctuations of the salinity level during a short period of time (a day, a month or a year), that takes place e.g. in modern estuaries connected both with the open sea and a freshwater basin (Odum, 1975). This reconciles the controversy between the absence of evaporates, restricted invertebrate assemblage, and the lack of plant remains as well as coarse-grained components of rock. The irregular rainwater-flow from land lowered the salinity level abruptly, but the tidal or constant connection of the Central Devonian Field with the main hypersaline basin, peculiar to that epoch (Rodionova, 1986), coupled with evaporation, raised it again.

The rich vertebrate assemblage is the result of high euryhaline abilities of these fishes in contrast to invertebrates that could not tolerate constant changes of living conditions.

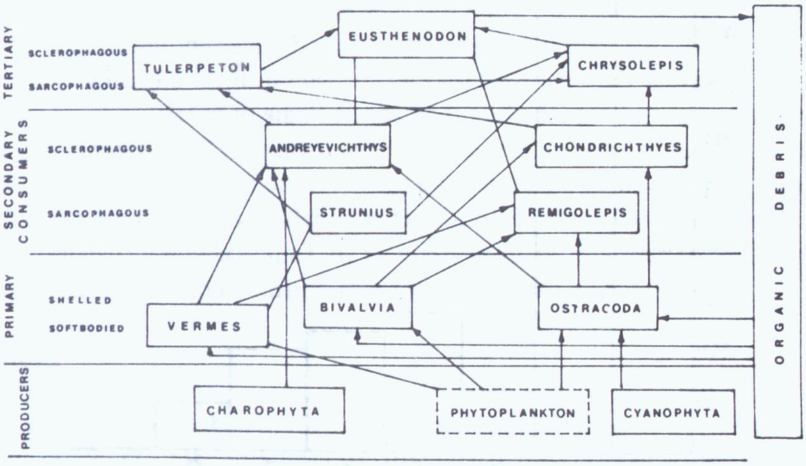
Mass mortality of fishes may have occurred as a result of the almost complete drying up of the basin. Water inflow was impossible at that time, and the subaqual maceration was fast.

All the assemblages containing the remains of *Remigolepis* (except in China) extend no further than 10° N and S from the equator (Scotese et al., 1985), which testifies to the constantly warm climate throughout the year.

The vertebrate community

The vertebrate remains constitute the greater part of the entire oryctocoenosis. The presumed autochthonous character of burial permits to restore the food- chain in the biocoenosis (Text-fig. 1)

Chondrichthyes. The chondrichthyan remains are represented by numerous tooth elements of the jaw symphysis and the jaw rami of an uncertain systematic position. It is not yet clear, whether these teeth belonged to the lower or the upper jaw, as all the symphysial dental plates are very similar and possess a horseshoe-shaped or subtriangular symmetrical base with the separate or partly

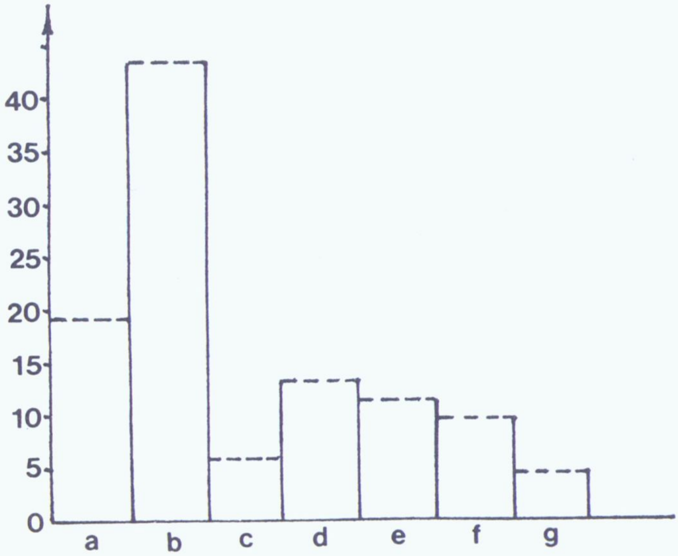


Text-fig. 1. Reconstruction of the presumed trophic connections in *Eusthenodon* assemblage of Andreyevka-2 locality. Phytoplankton, most probably present, is in a stippled box.
The main energy cycle passes through the organic debris and primary consumers. The reducents are not known.

fused dentine cusps. The easily visible worn surface is always somewhat concave. These elements cannot be attributed to any of the fossil chondrichthyan taxa, as their histology resembles more that of the dipnoans. As to the symphisial tooth elements, they have never been found in this group; however they are widely spread among chondrichthyans. This similarity in the feature is interpreted as a general construction that arose in the Devonian for the grinding purposes. The length of the fish was no more than 15-20 cm. There are 17 symphysial elements in the collections (Text-figs. 2, 3).

Antiarchi. The antiarch remains occur as the detached and partly jointed plates of the trunk armour, head shield, pectoral fins and parts of the tail squamation. They belong to a new *Remigolepis* species, *R. armata* (Lukševičs, 1991). The collection contains remains of about six individuals with the body length of about 40 cm.

Dipnoi. The dipnoan bones constitute the greater part of the entire bone mass. The total number of bones amounts to several hundreds. About 40 individuals can be used for the quantitative analysis, but there are also hundreds of upper and lower jaw tooth plates. The food specialization of *Andreyevichthys epitomus* Krupina changed during its lifetime (Krupina, this volume). The juveniles possessing the plates with pointed denticles probably fed on soft-bodied invertebrates, the adults



Text-fig. 2. The schematic representation of the minimum quantity of vertebrate individuals in the discrete mass of fossiliferous rock. The quantity was estimated by counting the separate unpaired or only left or right bones or tooth-element specimens. a - Chondrichthyes, b - *Andreyevichthys*, c - *Remigolepis*, d - *Strunius*, e - *Chrysolepis*, f - *Eusthenodon*, g - *Tulerpeton*.

could grind the shelly benthic invertebrates and charophyte algae, as the denticles became massive and the tips of the cusps turned blunt. The length of the adults was up to 50 cm.

Crossopterygii. There are three different crossopterygians participating in the food-chain. The smallest (30 cm long) is the benthophage *Strunius* sp., known by the numerous parasymphysial teeth and several fragments of jaw-bones. The long and pointed sigmoid teeth of the tooth-whorls could perhaps serve as tools for digging worms and other soft-bodied invertebrates out of the bottom mud. The pointed marginal jaw teeth served probably as grating tools to prevent the active prey from escaping. The number of individuals is estimated by the total amount of teeth divided by five —the average amount of parasymphysial teeth in *Strunius rolandi* (Gross), according to Jessen (1967).

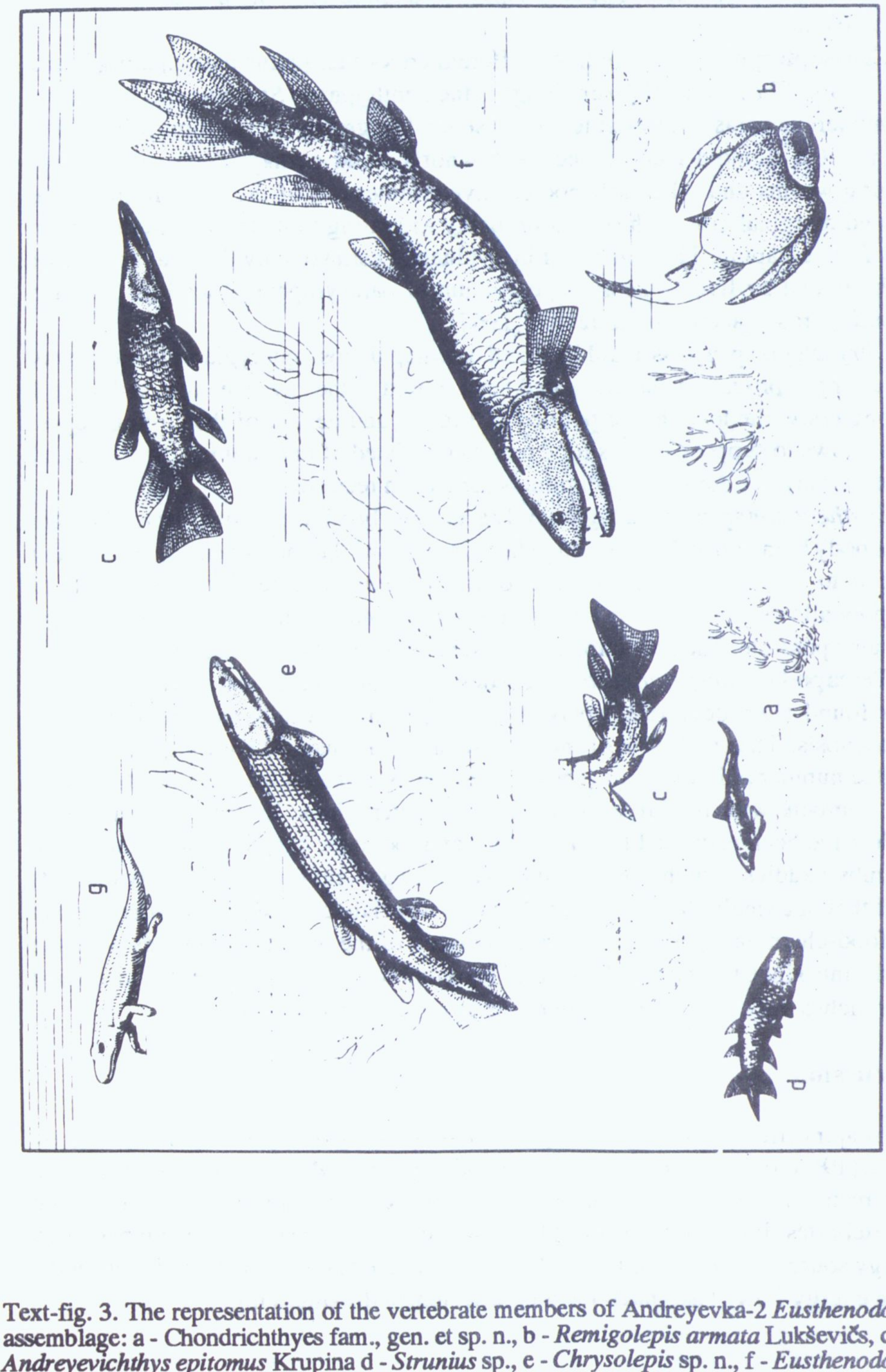
Chrysolepis sp. n. was a middle-sized osteolepid crossopterygian. Its active way of hunting is proved by the elongated head, round in the cross-section, and up to 1 m long body, the teeth being pointed and round and devoid of the cutting-edges. This allows to suppose that its food mostly consisted of unarmoured dipnoans and chondrichthyans. About 10 individuals have been recorded.

Eusthenodon sp. n. was a big, heavily armoured benthic predator, the total length of its body being up to 2 m. The huge fangs possessed the sharpened edges enabling the fish to bite through the carapaces of *Remigolepis*. The benthic mode of life of the prey allows to suggest its near-bottom living and hunting habits. Cannibalism was also possible. The collection contains the remains of more than 10 individuals.

Tetrapoda. *Tulerpeton curtum* Lebedev, being one of the most ancient tetrapods ever found (Lebedev, 1985) played an important but still unclear role in the biocoenosis. The small size of the animal (no more than 40 cm long) and a very limited number of individuals (about 5 specimens in the rock dissolved) did not let him compete with the large predatory crossopterygians. Its food specialization could have been restricted to small fishes and, perhaps, carrion. The construction of limbs-paddles with the elongated toes and the general form of the body reminds us of that of a small seal or an otter. A very unspecialized position of *Tulerpeton* in the food-chain may perhaps evidence in favour of the idea that tetrapods were the newly-introduced elements of the Late Devonian aquatic biocoenoses that occupied their niches only after small carnivorous arthrodires became extinct.

Discussion

The major difference of the Andreyevka assemblage from those described e.g. by Olson (1966, 1977) for the aquatic-terrestrial type of the Permian is the total absence of terrestrial plant debris. That is excluded from the food-chain as well as the aquatic invertebrates living on the water plants. Moreover, there seems to have been two energy sources — the organic and the inorganic; the plants were excluded from the main energy flow. That made the whole system selfmaintaining.



Text-fig. 3. The representation of the vertebrate members of Andreyevka-2 *Eusthenodon* assemblage: a - Chondrichthyes fam., gen. et sp. n., b - *Remigolepis armata* Lukševičs, c - *Andreyevichthys epitomus* Krupina d - *Strunius* sp., e - *Chrysolepis* sp. n., f - *Eusthenodon* sp. n., g - *Tulerpeton curtum* Lebedev.

The vegetable part of the assemblage consists of Charophyta and Cyanophyta. The only undocumented but apparently rather reasonable assumption is the presence of phytoplankton microorganisms in the water. The corresponding block is usually called the producers (Text-fig. 1). The major detritic food- sources are used by the aquatic invertebrates (ostracodes, worms and bivalves), i.e. the primary consumers. They could be divided into shelly (ostracodes, bivalves and sedentary worms) and soft- bodied (burrowing worms) forms. The alimentation type of the secondary consumers is reconstructed by studying their feeding apparatuses that are adapted either to crushing and grinding of shelly invertebrates (sclerophagous adult *Andreyevichthys* dipnoans and chondrichthyans) or to swallowing the soft-bodied ones and detritus from the bottom (sarcophagous and omnivorous *Remigólepis* and *Strunius*). The tertiary consumers are divided into sclerophagous (*Eusthenodon* that fed mostly on the armoured antiarchs and thick-scaled osteolepids) and sarcophagous predators, whose size was smaller and the swimming abilities were higher (*Chrysolepis* and *Tulerpeton*); the latter fed on dipnoans, chondrichthyans and small crossopterygians, including *Strunius*.

The comparison with another Devonian vertebrate assemblage of the Remigolepis Group in East Greenland (Spjeldnaes, 1982) has revealed no significant differences. The land-swamp side of Spjeldnaes's scheme is mostly based on the assumption that there existed some evident interconnection between the terrestrial and aquatic communities. The differences worth of note are: (1) the absence of the aquatic plants and invertebrates in East Greenland and (2) the absence of the terrestrial environments and, respectively, of land plants and invertebrates in Andreyevka palaeoenvironment. Still, the first may be interpreted by the sedimentological bias, whereas the second is notable. According to Spjeldnaes, *Ichthyostega* could feed both on fish in the aquatic environment and swamp, and on terrestrial arthropods that drew it to land. *Tulerpeton* did not have this feasible possibility, it had to feed and spawn in water, which means it was a completely aquatic animal.

The differences in the two secondary consumers' blocks are insignificant; the omnivorous dipnoans *Soederberghia* and *Jarvikia* being replaced by chondrichthyans and *Strunius*, with almost the same feeding habits. The name proposed for both communities is *Eusthenodon* community for the characteristic top-level carnivore.

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Palaeoichthyocenoses of the Famennian brackish seas of the Baltic area

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Abstract. The paper presents the results of palaeoecological studies of several Late Devonian, mainly Famennian vertebrate localities in Latvia. To differentiate the fishes as a part of the palaeobiocenosis the term "palaeoichthyocenosis" is proposed. Main attention has been paid to the analysis of ecological characteristics of agnathans and fishes, and to their interrelations in the palaeoichthyocenoses of the Late Devonian brackish seas in the East Baltic area. It has been shown that the structure of the palaeoichthyocenoses remained practically unchanged at least from the end of the Frasnian to the end of the Famennian, although their species composition changed considerably. The assemblages are characterized by high species diversity of predatory fishes. Evidently the similar palaeoichthyocenoses were fairly wide-spread in the Late Devonian epicontinental seas.

During the last twenty years some stratigraphers and palaeontologists (L. Lyarskaya, V. Sorokin, E. Lukševičs, O. Lebedev, N. Krupina) have collected a large number of fish remains from the Upper Devonian localities of the East Baltic region. The results of the research concerning mainly the Famennian localities are discussed in the paper. Principal attention is paid to the analysis of the ecological features of fishes and their interrelation in the range of palaeoichthycenoses of the brackish seas.

Fish community, being a part of a biocenosis and inhabiting a common biotope, was termed as ichthyocenosis (Parin, 1988). Fish community as a part of an extinct, ancient biocenosis is suggested to be called palaeoichthyocenosis. This term is the most explicit and precise for the description of ancient biocenoses based on fish remains only, as the environmental conditions might have been unfavourable to fossilization of other animals and plants.

It is quite evident that one taphocenosis might have included fish fossils from various palaeoichthyocenoses. And, vice versa, under the influence of diverse taphonomic factors, one ancient ichthyocenosis might have produced more than one local taphocenosis. This statement is confirmed by the following example.

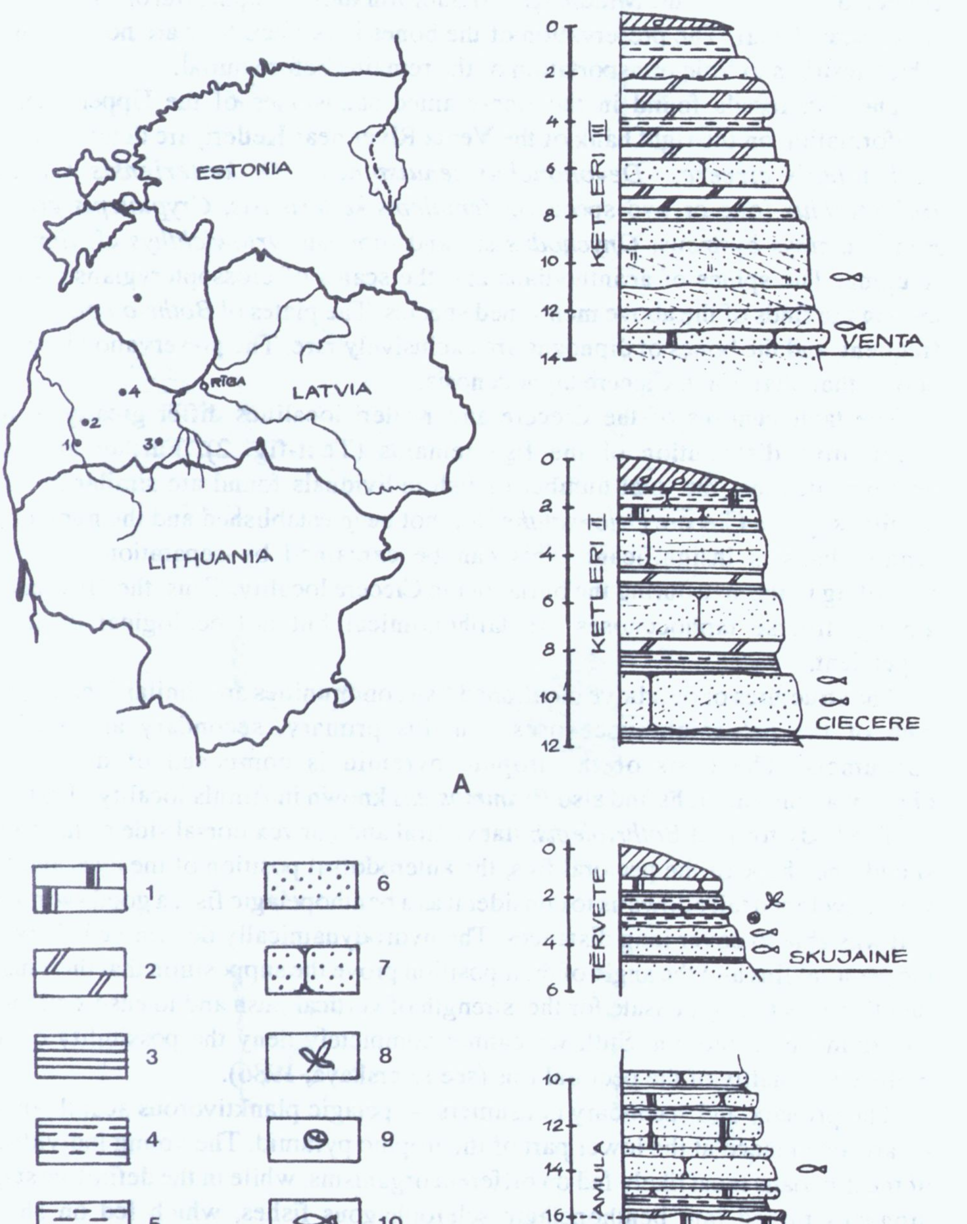
All the Devonian seas of the Baltic region were located on the continental shelf, thus being epicontinental and comparatively shallow. During the transgression process the facies zonation of the Late Devonian seas became more uniform getting more complicated at the regression period. During the regression the facial changeability increased and the seas with abnormal salinity expanded. The author has investigated the structure of the palaeoichthyocenoses of three basins of lowered salinity dating back from the end of the Frasnian to the end of the Famennian.

At the end of the Frasnian the area of seas diminished, so in the Amula time the normal salinity marine deposits were not produced (Savvaitova, 1977). The outcrop on the left bank of the Amula River is the stratotype of the Amula Beds (Text-fig. 1). Sands and sandstones, intercalated by siltstones and silty dolomites, contain here the accumulations of fish and agnathan remains, lingulids and conchostracans. Invertebrates belong to euryhaline groups, adapted to living in shallow waters. As to the manner of nutrition, they were filtrators and detrivores. The fish community of the coastal part of the Amula Sea was comparatively rich and included antiarchs *Bothriolepis* sp. and *Taeniolepis* sp., undetermined arthrodires, psammosteids *Psammosteus* cf. *tenuis* Obr. and *Psammosteus* sp., numerous *Holoptychius* cf. *nobilissimus* Ag., and a rare undetermined osteolepid, acanthodian *Devononchus laevis* Gross, and *Dipterus*-like dipnoans.

The section on the Skujaine River near Klūnas, the stratotype of the Tervete Beds, consists of rhythmical intercalations of sands, dolomitic marls and siltstones. Deposits of the basins with the normal salinity were missing throughout the Tervete time (Savvaitova, 1977). One may find the mass accumulation of oogonia of charophytes as well as fish bones in the sand. The traces of burrowing organisms *Rhizocorallium* and plants may be recorded in the interlayers of dolomitic marls and siltstones.

The palaeoichthyocenosis of the Tervete brackish sea is more diversified than that of the Amula Sea and includes placoderms, acanthodians, crossopterygians and dipnoans. The preservation of bones is satisfactory, more than 25 per cent of the material being represented by undestroyed, insignificantly deformed plates of placoderms, and some bigger crossopterygian bones. The bones are rounded to various degrees. Skull fragments are usually found disintegrated, yet whole head shields of bothriolepids have also been found. This allows to conclude that the post mortem transportation of the remains had not been considerable. The remains of crossopterygians: scales, skull-bones and teeth of *Holoptychius* cf. *nobilissimus* Ag., *H.* cf. *giganteus* Ag., *Platycephalichthys skuenicus* Vorob. and *Cryptolepis* sp. are most frequent. The finds of the placoderms and acanthodians are less numerous, e.g. those of *Phyllolepis tolli* Vasil., *Bothriolepis ornata* Eichw. and *B. jani* Lukš. the spines of *Devononchus tenuispinus* Gross are found more often than those of *Homacanthus sweteensis* Gross, *Chelyophorus* sp. and *Dunkleosteus* sp., as well as tooth plates of *Dipterus* sp. and *Conchodus* sp. are rare.

At the coastal region of the Middle-Late Ketleri shallow sea rhythmic deposition of sands interbedded with siltstones, clays and dolomite marls took place (Lyarskaya and Savvaitova, 1974). This taphocenosis contains numerous (and prevailing) intact parts of trunk and head shields, pectoral fins and separate bones of *Bothriolepis ciecere* Lyarsk.; rare spines and scales of *Devononchus* sp.; skull and shoulder girdle bones and scales of *Holoptychius* sp.; rare scales of *Ventalepis ketleriensis* Schultze; bones of the skull, lower jaw and some scales of *Cryptolepis grossi* Vorob. and *Panderichthys bystrowi* Gross; rare scales of *Onychodus* sp.; vertebrae and teeth of several crossopterygians. Remains of these forms can be



Text-fig. 1. Sketch-map showing the localities of the Late Devonian vertebrates of the brackish seas of the Baltic area (A) and their sections (B). Sections after Savvaitova (1977) and the author of the present paper. A: 1 - Ketleri, 2 - Ciecere, 3 - Skujaine, 4 - Amula; B: 1 - dolomite, 2 - dolomitic marl, 3 - clay, 4 - clayey siltstone, 5 - siltstone, 6 - sand, 7 - sandstone, 8 - plants, 9 - oogania of charophytes, 10 - fishes.

collected from sand of the Middle Ketleri Subformation cropping out on the Ciecere River near Pavari. The preservation of the bones is perfect, they are not rounded, which testifies to little transportation of the remains before burial.

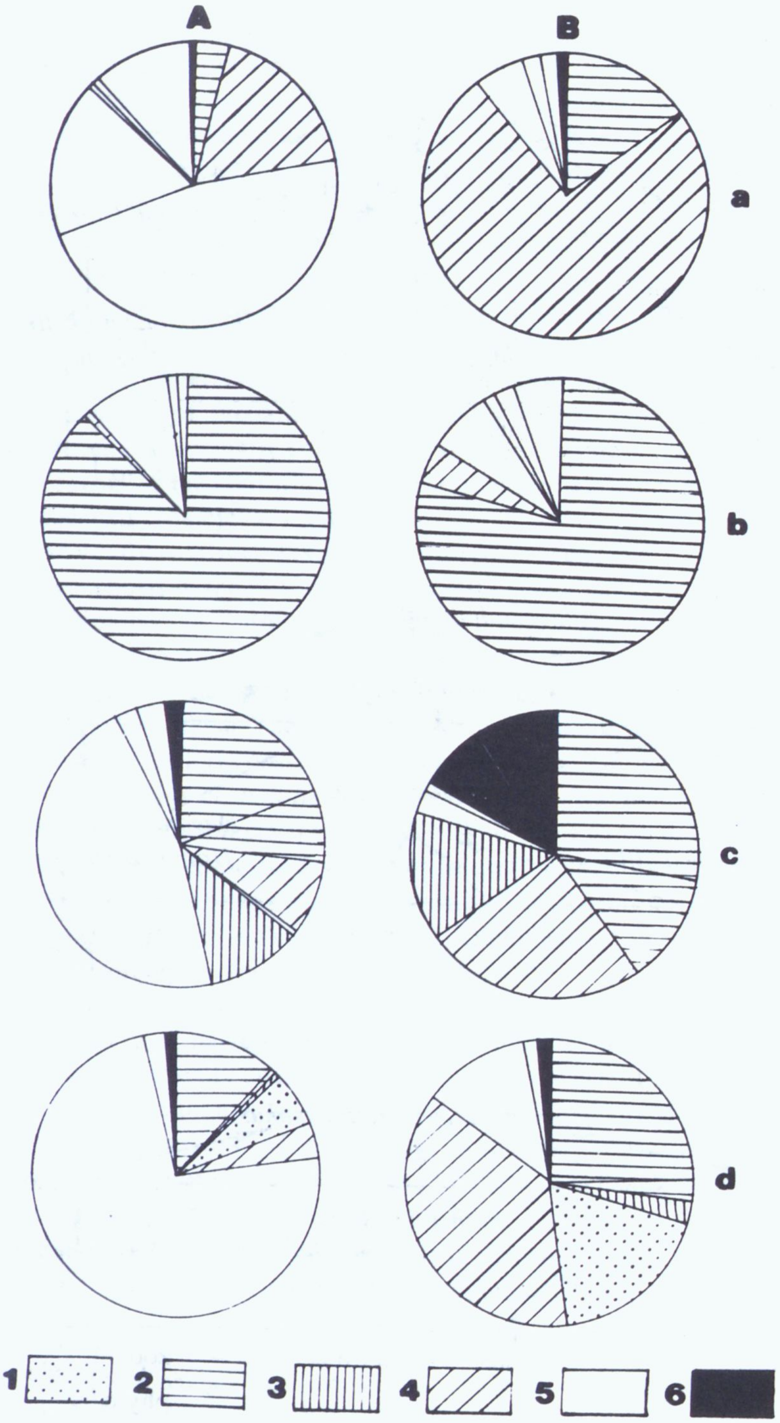
The fish fossils found in the fine-grained sandstones of the Upper Ketleri Subformation on the right bank of the Venta River near Ketleri, are determined as *Bothriolepis ciecere*, *Devononchus tenuispinus*, *D. ketleriensis* Gross, *Holoptychius* (one or two species), *Ventalepis ketleriensis*, *Cryptolepis grossi*, *Panderichthys bystrowi*, *Onychodus* sp. and dipnoan *Orlowichthys* cf. *limnatis* Krupina. The spines of acanthodians and the scales of crossopterygians prevail among the finds of the above mentioned species. The plates of *Bothriolepis* are not frequent, and the bones of dipnoans are exclusively rare. The preservation is much poorer than that of the Ciecere taphocenosis.

The taphocenoses of the Ciecere and Ketleri localities differ greatly in the quantitative distribution of the fish remains (Text-fig. 2). Further analysis demonstrates that the total number of fish individuals found are similar in both localities, yet in Ciecere *Orlowichthys* has not been established and the number of acanthodians is insignificant. This can be explained by separation of bones according to the size during the burial in the Ciecere locality. Thus, the differences among diverse taphocenoses are taphonomical but not ecological or time-dependent.

The structures of the above mentioned fish communities are similar. The trophic web of the palaeoichthyocenoses contains primary, secondary and tertiary consumers. The basis of the trophic pyramid is composed of detrito- or phytophagous antiarchs and also *Psammosteus* known in Amula locality (Text-fig. 3). The body form of *Bothriolepis*: flat ventral and convex dorsal side of the trunk shield, the shape of the pectoral fins, the anterodorsal position of the eyes and the well-developed tail allows us to consider it as a benthopelagic fish, a good swimmer that was able to cover long distances. The hydrodynamically determined shape of the pectoral fins and the angle of their position prove the supposition that their main function was to compensate for the strength of vertical push and to ensure vertical and roundabout motion. Still, we cannot completely deny the possibility of the multifunctionality of the pectoral fins (see Lyarskaya, 1986).

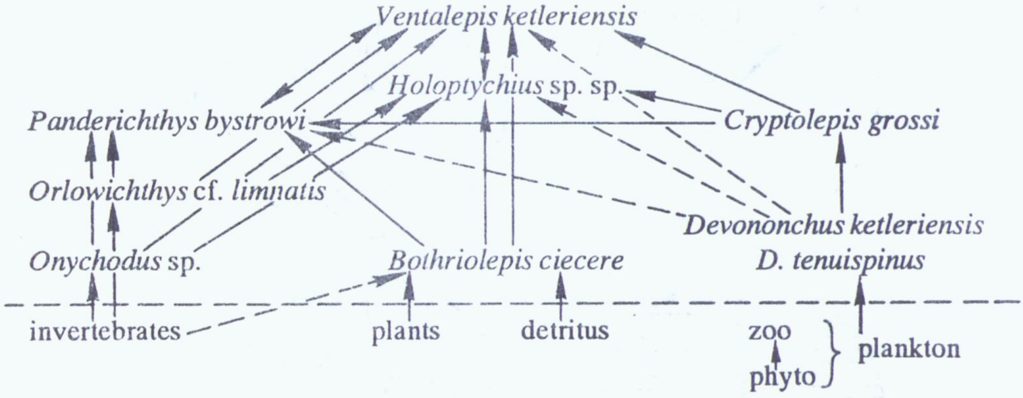
The primary and secondary consumers — pelagic planktivorous acanthodians — are also placed at the lower part of the trophic pyramid. The young individuals of the dipnoans most likely fed on different organisms, while in the definitive stage dipnoans turned into benthopelagic sclerophagous fishes, which fed on shelly invertebrates (see Krupina, this volume). In the Tervete assemblage this ecological niche was also occupied by *Chelyophorus*. As to *Onychodus*, Lebedev has suggested that with the help of parasymphysial teeth they could out the soft-bodied invertebrate infauna out of the bottom sediment (Novitskaya, Talimaa and Lebedev, 1983).

The ecological niches of the pelagic predators are filled in the all three ichthyocenoses. They were medium-sized osteolepid and *Cryptolepis*, hunting

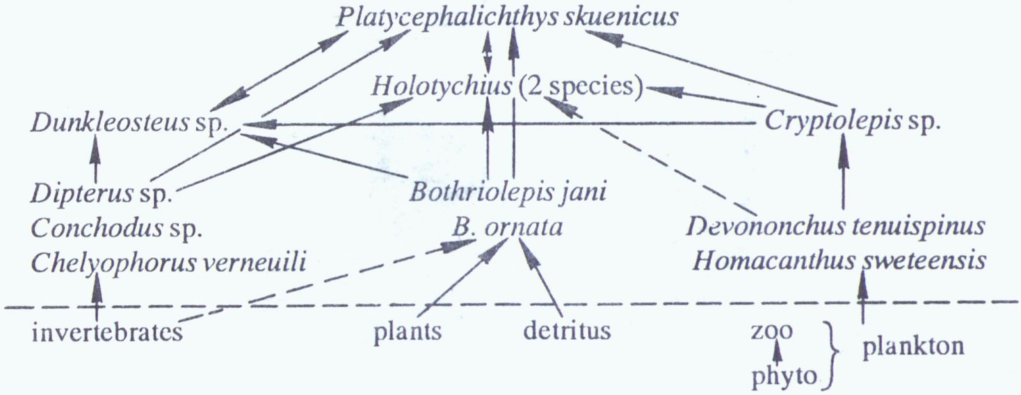


Text-fig. 2. Quantitative distribution of fish remains (A) and individuals (B) in the Upper Devonian fish localities of the Baltic area. a - Ketleri, b - Ciecere, c - Skujaine, d - Amula; 1 - psammosteids, 2 - antiarchs, 3 - arthrodires, 4 - acanthodians, 5 - crossopterygians, 6 - dipnoans.

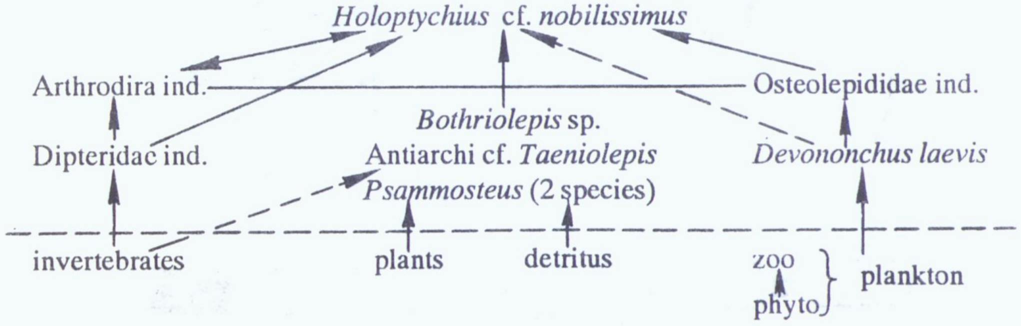
Ketleri – Ciecere



Skujaine



Amula



Text-fig. 3. Scheme of the fish interrelations in the palaeoichthyocenoses of the Upper Devonian brackish seas of the Baltic area. Arrows show the main relations.

actively on the juvenile dipnoans and acanthodians in the whole water-body. The pike-like pelagic predators-ambuscaders which occupied the top of the trophic pyramid, i.e. holoptychiids and *Platycephalichthys* fed on big, mobile prey, mainly on antiarchs and psammosteids but also on other fishes, including predators. During the Ketleri age the niche of the bottom-living predator-ambuscader of the contemporary sheat-fish type was occupied by *Panderichthys*, which had a flat skull with dorsally set eyes. Large arthrodires and *Phyllolepis* are also believed to belong to this type (Long, 1984).

For all three ichthyocenoses, despite striking differences in the quantitative distribution of fish remains, the prevalence of non-predatory fishes is characteristic. As to our most approximate estimations, the number of non-carnivorous fish exceeds the number of predators by four and a half to nine times. Thus, the ecological pyramid is normally constructed, and some of the ecologists consider it to testify in favour of the conformity of the structure of a palaeocommunity to the given taphocenosis (Malejeva, 1984).

The above-described fish communities resemble the Rybnica palaeoichthyocenosis in the Orel Region (Russia) investigated by N. Krupina and O. Lebedev (Novitskaya, Talimaa and Lebedev, 1983). The authors consider that this Late Devonian locality has been formed in the deltaic environment, under the influence of frequently changing hydrodynamic conditions and changeable salinity tending to become brackish. The structure of the palaeoichthyocenosis of Rybnica resembles that of Ketleri, possessing common or similar taxa: *Panderichthys bystrowi*, *Holoptychius* cf. *nobilissimus* and *Orlowichthys limnatis*. The specific characteristics of *Bothriolepis* from Rybnica still need to be determined, as *B. ornata* has not been redescribed yet. *Chrysolepis orlensis* Lebedev is close to *Cryptolepis grossi* (Lebedev, pers. comm.). The differences between the palaeoichthyocenoses lie in the absence of *Ventalepis* and in the occurrence of *Chelyophorus* in Rybnitsa (not discovered in Ketleri).

The material under discussion leads to the following **conclusions.**

1. The structure of palaeoichthyocenoses of brackish seas in the East Baltic region remained practically unchanged at least from the end of the Frasnian till the end of the Famennian,though the correlations of species changed greatly.
2. The large variety of predatory fishes is characteristic of the palaeoichthyocenoses of the Late Devonian brackish seas of the Baltic area.
3. Similar palaeoichthyocenoses may have been quite common to the epicontinental seas of the Late Devonian.

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Fish assemblages and facies in the Telengitian Suprahorizon of Salair

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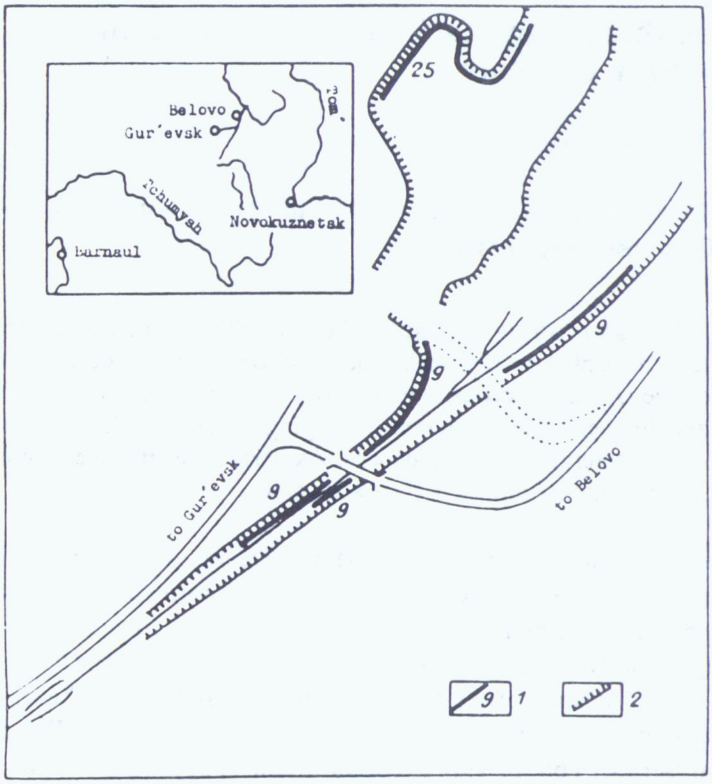
Abstract. In the paper fish assemblages of the Telengitian Suprahorizon, constituting an approximate equivalent of the Emsian in Salair, are considered. Three facies: organogenic-clastic limestone (A), argillaceous limestone (B) and laminated limestone (C) facies are characterized by vertebrate remains belonging to acanthodians, elasmobranchs, placoderms, crossopterygians, and dipnoans. Associated invertebrates are indicated and possible environmental conditions of faunas are given.

Stratotypical sections of the Lower and Middle Devonian units in Salair are located in the vicinity of Gur'evsk (Text-fig. 1.). These units correspond to the stratigraphic interval approximating to the Emsian Stage (Text-fig. 2.) In recent years it has been thoroughly studied in order to solve the problem of the Lower and Middle Devonian boundary. In the scheme of the Salair Devonian stratigraphy it bears the name of the Telengitian Suprahorizon and is attributed to the Middle Devonian or the Shirdagian Series (Yolkin, 1985; Yolkin et al., 1988). Fish remains, as well as ostracodes and scolecodonts were discovered by dissolving carbonate rocks in the acetic acid for conodonts. Fishes are preserved as isolated skeletal elements: scales, teeth and bone fragments belonging to Acanthodei, Elasmobranchii, Bradyodonti and also to Crossopterygii and Dipnoi, rarely to Placodermi.

A detailed description of sections of the Salairka, Belovo and Shanda horizons forming the Telengitian Suprahorizon, has been given by Yolkin et al. (1988). They have presented a complete facies profile model for the Telengitian deposits, showing the lateral and vertical transitions of facies within a small area of the Krekov Syncline. The rocks of the Telengitian interval are arranged in four groups (facies) by their lithogenous features: organogenic-clastic limestone (A), argillaceous limestone (B), the facies of laminated limestone (C) and sandy argillite (D) (Text-fig. 3).

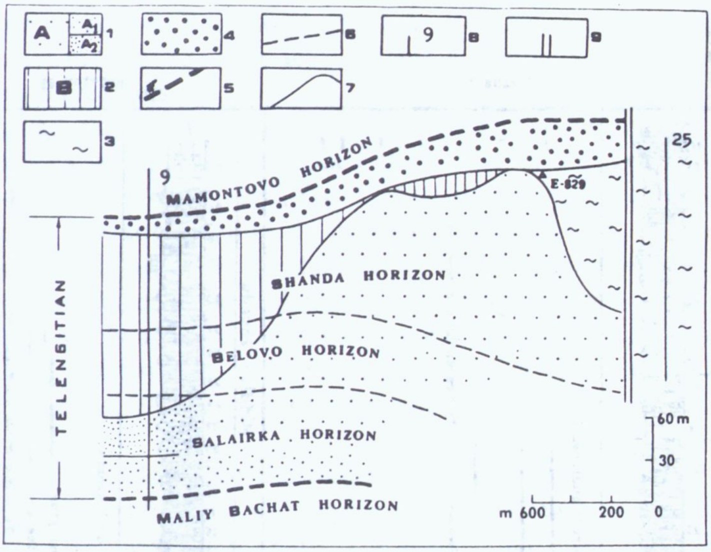
The distribution of fishes and their association with some other groups depending on the environmental conditions is exemplified on sections 9 and 25, where the Telengitian Suprahorizon is represented by all of its subdivisions and the whole set of facies (Text-figs. 1, 4). In the early Salairka time, the accumulation of extremely shallow water terrigenous-carbonate sediments took place in the near-shore zone. The corresponding rocks include both animal and plant fossils (subfacies A_1; beds 7-10 of section 9). In a shallow water zone on a "carbonate platform" mainly organogenic clastic carbonate mud (subfacies A_2; beds 11-14 of section 9) accumulated.



Text-fig. 1. Location of the sections. 1 - sections, 2 - outcrops.

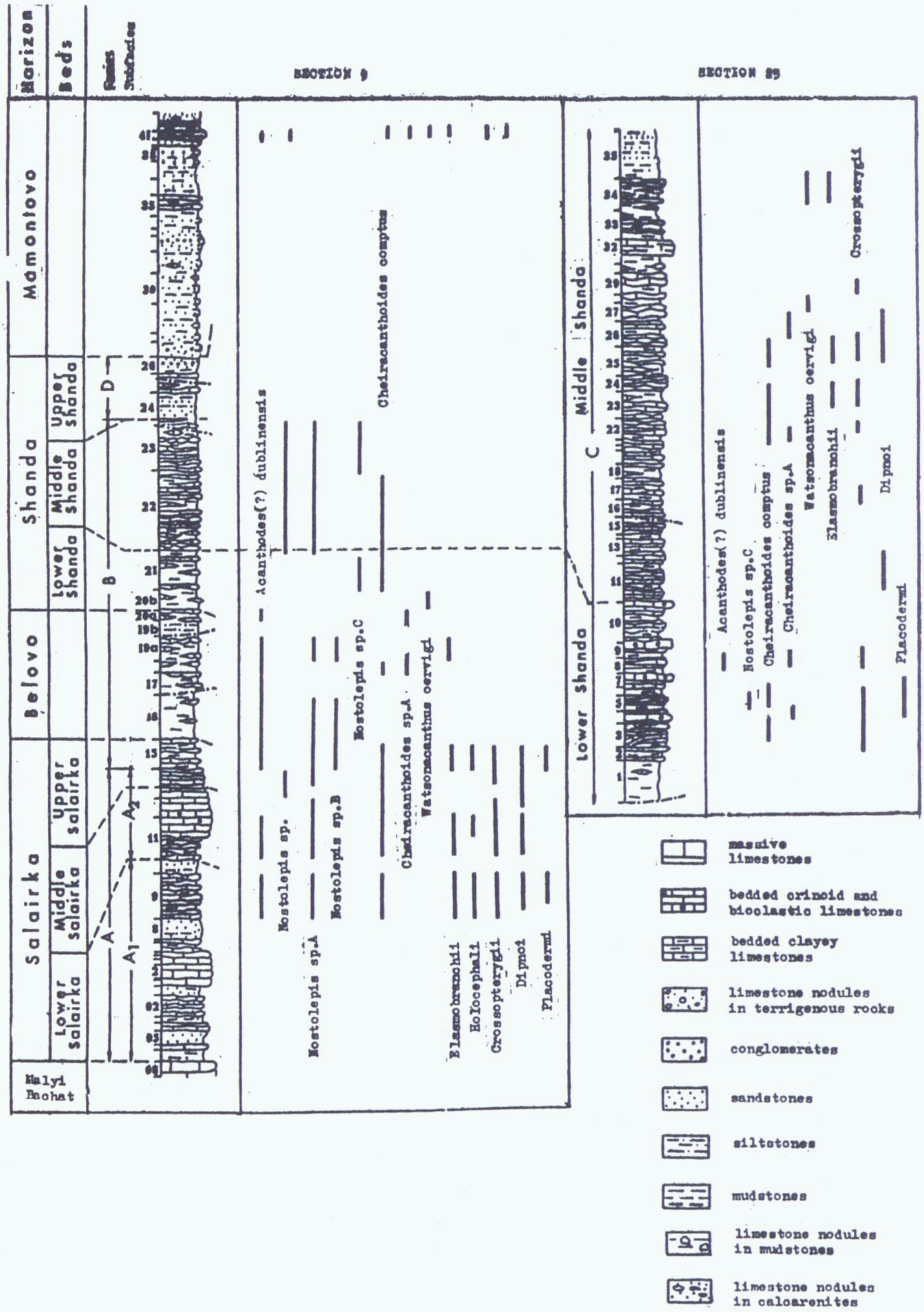
SHIRDAGIAN (Middle Devonian - D_2)	TELEUTIAN			[c. costatus]
	TELENGITIAN	Shanda Horizon	Upper Shanda Beds	[c. partitus c. patulus]
			Middle Shanda Beds	serotinus
			Lower Shanda Beds	inversus P.sp.n."P.aff.P.perbonus"
		Belovo Horizon		gronbergi
		Salairka Horizon	Upper Salairka Beds	dehiscens
			Middle Salairka Beds	
			Lower Salairka Beds	
MADMONIAN (D_1)	BELTIRIAN			[pireneae sulcatus]

Text-fig. 2. Subdivisions of the Telengitian Suprahorizon at its type locality (from Yolkin et al., 1988).



Text-fig. 3. Schematic facial profile of the Telengitian Suprahorizon near Gur'evsk. 9, 25 - studied sections (see explanation of Text-fig. 4). 1 - facies A and subfacies A_1 and A_2; 2 - facies B; 3 - facies C; 4 - facies D; 5 - stage boundaries; 6 - horizon boundaries; 7 - facies and subfacies boundaries; 8 - location of studied sections; 9 - fault zone (slightly modified after Yolkin et al., 1988).

The enrichment of the fauna, including fishes, took place in the late early Salairka time (bed 9 of section 9), probably, indicating the stable marine regime. Since then, environmental conditions in the Salair basin were favourable for many groups of benthic organisms adapted to life in shallow water. Brachiopods are represented by anchored and free-lying forms: pentamerids, spiriferids, leptaenids, etc. which make up separate coquina beds. Trilobites, ostracodes, gastropods, rugose and tabulate corals (often rock-forming), bryozoans and crinoids have been recorded (Yolkin et al., 1988). Pelagic organisms include conodonts (*Panderodus*, *Icriodus*, *Panderinellina*) and scolecodonts. Fishes are mostly represented by acanthodians (Text-fig. 4; Pl. I). Most of them range practically through the whole Telengitian Suprahorizon. In the acanthodian assemblage the scales of *Acanthodes* (?) *dublinensis* Stauffer, *Nostolepis* sp. A. and *Cheiracanthoides comptus* Wells predominate. The taxonomical diversity of other fishes is low. Among chondrichthyan remains the scales of elasmobranchs prevail. Crossopterygii are represented by struniiforms and dipnoans by *Dipterus*, preserved as scales and small fragments of bones. The fishes under consideration may serve as indicators of the shallow water marine environments. Of placoderm remains fragments of radotinid tesserae are present. The faunal diversity of the Salairka basin may have been caused by the abundance of nutrients. Certain food relations were developed between the organisms: brachiopods (filtrators), trilobites and ostracodes (detrivores) and gastropods (predators) had swimming larvae, which together with worms and conodont-animals, small invertebrate benthic organisms, plant remains, and



Text-fig. 4. Stratigraphic distribution of the fish in sections9 and 25 of the Telengitian Suprahorizon of Salair.

seaweeds were the main food for fish. Besides, according to Novitskaya (Novitskaya et al., 1983) large acanthodians, crossopterygians and elasmobranchs belonged to predators.

In the late early Salairka time an isolated trough started to form on the Krekov Syncline area, which later during the Belovo- Shanda time gradually turned into a depression (Yolkin et al., 1985, Fig. 5). Alterations in sedimentation caused great changes in the composition of deposits. Consequently, greenish-brown or yellowish-brown argillites are dominating in the section, whereas fossiliferous limestones of facies B are subordinate (Text-fig. 4, beds 15-23 of section 9). Considerable changes in the faunal assemblages were due to those in the environments. Obviously at the initial period of the formation of the depression (bed 15 of section 9), the earlier food relations remained and the fish assemblage did not change.

Later, in the Belovo time the accumulation of deposits, forming afterwards the argillite-limestone facies B, was in progress. Only a few acanthodian remains have been found among the fish fossils. The acanthodian assemblage did not change. The appearance of *Nostolepis* sp. and *Cheiracanthoides* sp. A may evidence that these forms preferred environments related with to facies B (Pl. II). Enriched with terrigenous suspension, muddy, poorly aerated waters of the depression were not suitable for corals, bryozoans and trilobites. The environment with low hydrodynamical activity was favourable for organisms specially adapted to dwelling on a soft silty ground. The systematic composition of brachiopod assemblages became much more restricted though free-lying forms or those attached to seaweeds, i.e. chonetids, orthids and rhynchonellids were abundant enough to make up bank-type colonies. In some layers brachiopods were rock-forming. As compared to the Salairka ostracode assemblage of facies A, the assemblage of siliceous ostracodes typical of facies B is poorer and less diverse. In addition to the conodonts known from the underlying rocks, *Polygnathus gronbergi* Klapper et Johnson has been found (Yolkin et al., 1988).

In the Shanda time on the slope in the shallow zone other sediments than in facies B started to accumulate. They are represented by thin-bedded clayey limestones with well-defined traces of subaqueous slumping (Text-fig. 4, facies C of section 25). Brachiopods, ostracodes, rugose corals, trilobites, and other fossils can be met with more or less uniformly throughout the sections and in the rocks. Secondary accumulations of the organic remains are lacking, except those of crinoid columnals occurring in some beds and layers. Yet, the environments were favourable for fishes. Their remains are much more varied in the rocks of facies C than in the contemporaneous facies B. They belong to the acanthodians *Cheiracanthoides comptus* Wells, *Watsonacanthus oervigi* Valiuk., and *Acanthodes* (?) *dublinensis* Stauffer, more rarely to *Nostolepis*. The appearance of elasmobranchs is noteworthy for that time, scales of which differ from those found in rocks of facies A. Of other groups Crossopterygii, Dipnoi and Placodermi (?) occur (Text-fig. 4; Pl. III).

In late Shanda time sandy-clayey deposits of facies D accumulated in a temporarily dried up near-shore zone (Text-fig. 4, beds 25, 26 of section 9). For most of the organisms the living conditions were not favourable. Conodonts, scolecodonts and fishes are completely absent. Only plant remains are numerous.

The above analysis of the distribution of fishes and other organisms in the Telegitian Suprahorizon sections allows us to emphasize substantial ecological factors influencing the composition of the faunal assemblages. This has confirmed the conclusion by Valiukevicius (1985) that the vertical distribution of acanthodians is only slightly dependent on the facies pattern of deposits, which makes them highly valuable for stratigraphy.

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Plate I. Vertebrate fossils from the facies A.

Figs. 1-19 - Acanthodian scales: 1, 2 - *Acanthodes* (?) *dublinensis* Stauffer, B-829-9; 3-5 - *Nostolepis* sp. A. 3,4 - Ya-869-12/1, 5 B-819-9/1; 6-10 - *Nostolepis* sp. B. 6 - Ya-869-13/2, 7-10 - B-829-9; 11-15 - *Nostolepis* sp. 11 - B-829-9, 12 Ya-869-12/1, 13 - B-829-9, 14 - Ya-869-12/1, 15 - B-829-9; 16-19 - *Cheiracanthoides comptus* Wells. 16 - B- 819-13/1, 17-19 - B-829-9 Figs. 20-22 - Scale and teeth of Elasmobranchii. 20,21 - Ya-869-12/1, 22 - Ya-869-11/5 (for all x 40).

Fig. 23 - Articulated scales of Dipnoi. B-919-14/1 (x 20).

Fig. 24 - Struniiform crossopterygian tooth. B-819-9/7 (x 40). Figs. 25, 26 - Placoderm remains. 25 - *Ohioaspis* (?) sp. Ya-869-11/5 (x 40), 26 - fragment of Radotinida, Ya-869-11/3 (x 30).

Plate II. Vertebrate fossils from the Facies B.

Figs. 1-18 - Acanthodian scales: 1 - *Acanthodes* (?) *dublinensis* Stauffer, B-819-20/3 (x50); 2-5 - *Nostolepis* sp. A, B-829-15; 6-8 - *Nostolepis* sp., B, 6 - B-829-15, 7 - B-819-22/2, 8 - B-809-23b (for all x 40); 9 - *Nostolepis* sp. B-819-23/3 (x 50); 10-12 - *Watsonacanthus oervigi* Valiuk. 10 - B-819-19/3 (x 30), 11 - B-819-20/8 (x 40), 12 - B-819-23/3 (x 40); 13-15 - *Cheiracanthoides comptus* Wells, 13 - B-829-15 (x 20), 14 - B-819-19/3 (x 20), 15 - B-819-22/2 (x 40); 16-18 - *Cheiracanthoides* sp. A, 16 - B-829-15 (x 40), 17 - B-819-19/4, 18 - B-819-21/6 (for all x 50).

Fig. 19 - Placoderm scale B-819-18/2; 19a - in lateral view, 19b - in external view, (x 40).

Fig. 20 - Dipnoan scales. B-829-15 (x 30).

Figs. 21, 22 - Crossopterygian remains. 21 - B-819-20/11 (x 20), 22 - B-829-15 (x 30).

Plate III. Vertebrate fossils from the facies C.

Figs. 1-10 - Acanthodian scales: 1 - *Nostolepis* sp. B, B- 8225-14(22)[*] (x 40); 2-4 - *Nostolepis*-like scales, 2 - B- 8225-14(22) (x 20), 3 - B-8225-31/1(5), 4 - B-8225-11(25); 5-7 - *Watsonacanthus oervigi* Valiuk. 5 - B-8225-2(34), 6 - B- 8225-33a(3.2), 7 - B-8225-14(22); 8-10 - *Cheiracanthoides comptus* Wells, 7,8 - B-8225-14(22), 9 - B-8225-11(25) (for all x 40), 10 - B-8225-11(25) (x 50).

Figs. 11-17 - Scales of Elasmobranchii. 11-14 - B-8225-11(25); 15a, b - B-8225-11(25); 15a - in external view, 15b - in basal view; 16 a, b - B-8225-11(25); 16a - in external view, 16b - in basal view (for all x 50), 17 - B-8225-14(22) (x 30).

Figs. 18-24 - Fragments of crossopterygian scales and mandible. 18 - B-8225-33a(3.2), 19 - B-8225-11(25), 20 - B-8225-25(11) (for all x 40), 21 - B-8225-30(6) (x 20); 22 - *Onychodus* sp., B- 8225-31/2(5) (x 20), 23, 24 - Struniiform crossopterygian teeth: 23 - B-8225-11(25) (x 30), 24 - B-8225-11(25) (x 20).

Fig. 25 - Dipnoan scale, B-8225-32/2(4) (x 20).

Fig. 26 - Scale of *Ohioaspis* sp., B-8225-14(22) (x 20).

[*] B-8225-14(22): B-8225-14 - specimen number (field number of the bed), (22) - bed number.

Plate I

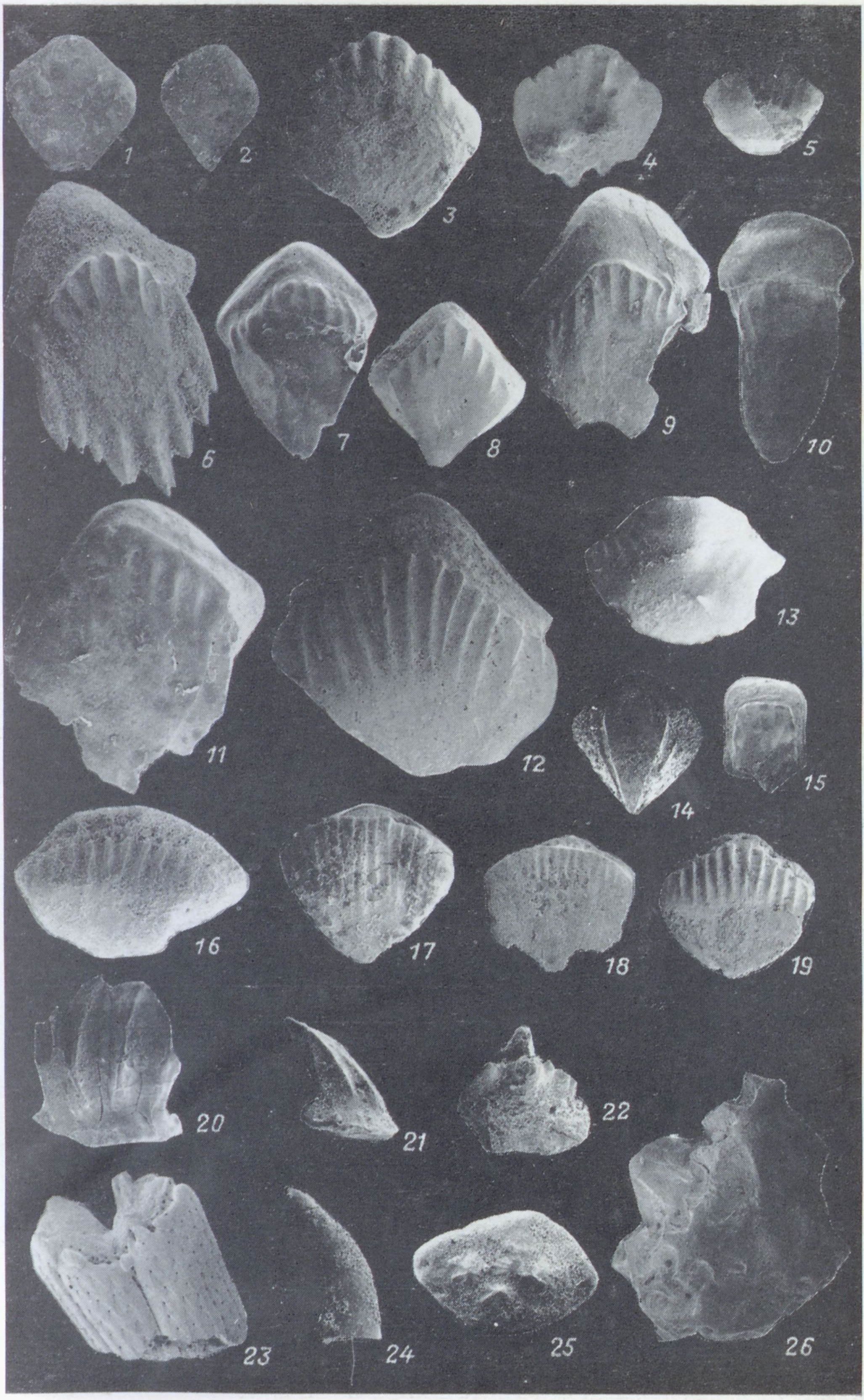

Plate II


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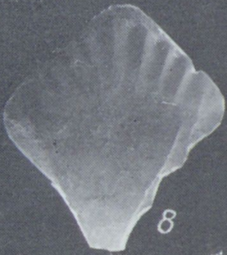
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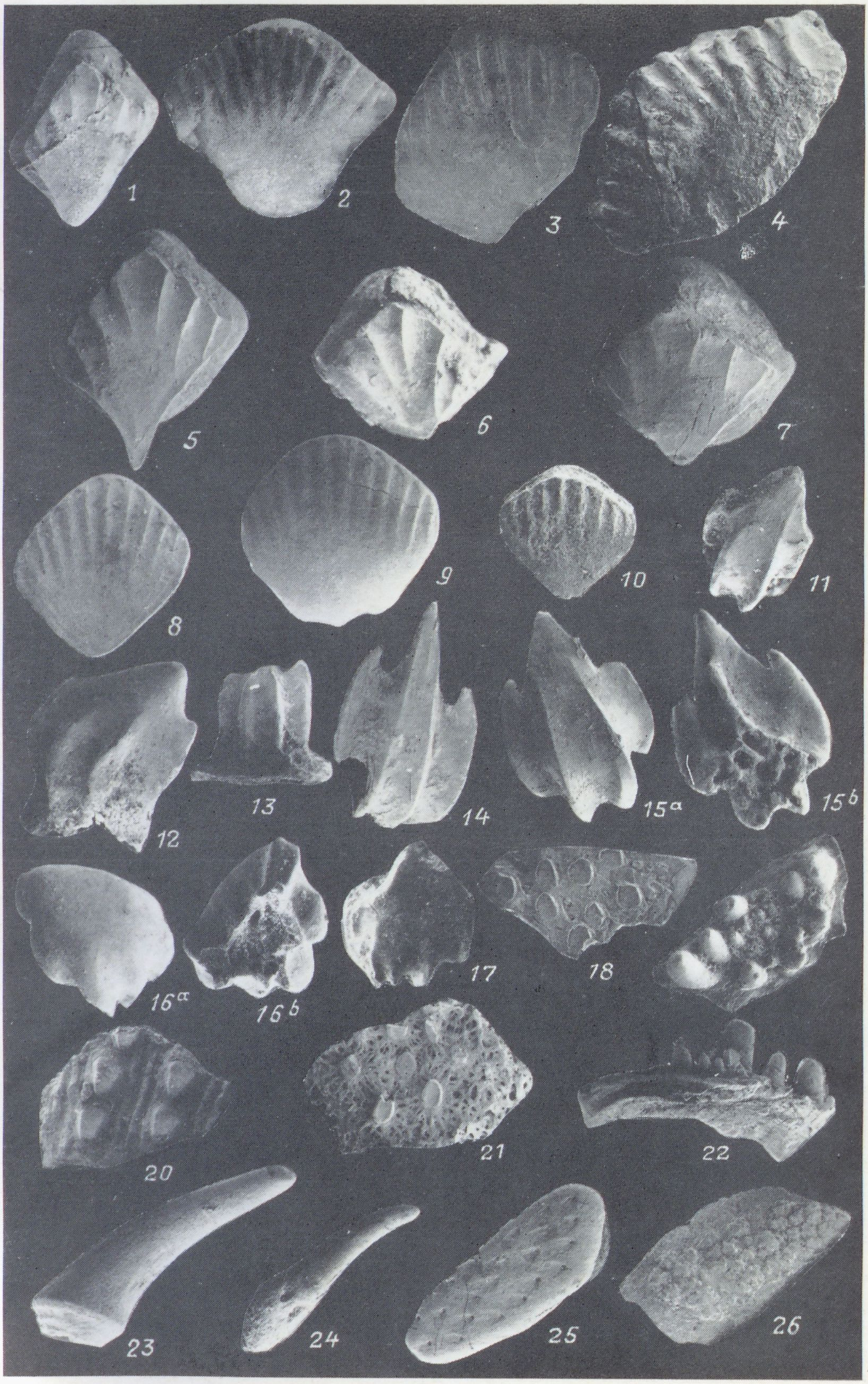
Plate III



The Late Permian ichthyofauna from the east of the Russian Platform and Pre-Urals from systematic and ecological- palaeogeographical aspects

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Abstract. The paper gives a review of the taxonomic composition of the Late Permian ichthyofauna on the east of the Russian Platform and West Pre-Urals. Finds of elasmobranchs (*Wodnika*, *Ctenacanthus*, *Xenosynechodus*, etc.), holocephalians (IJanassa), dipnoans (*Gnathorhiza*), and numerous actinopterygians of five orders (Palaeonisciformes, Elonichthiformes, Cheirolepidiformes, Eurynotoidiformes, Platysomiformes) have been recorded.

For stratigraphical purposes well-identifiable fragments of eurynotoids and platysomids can be used.

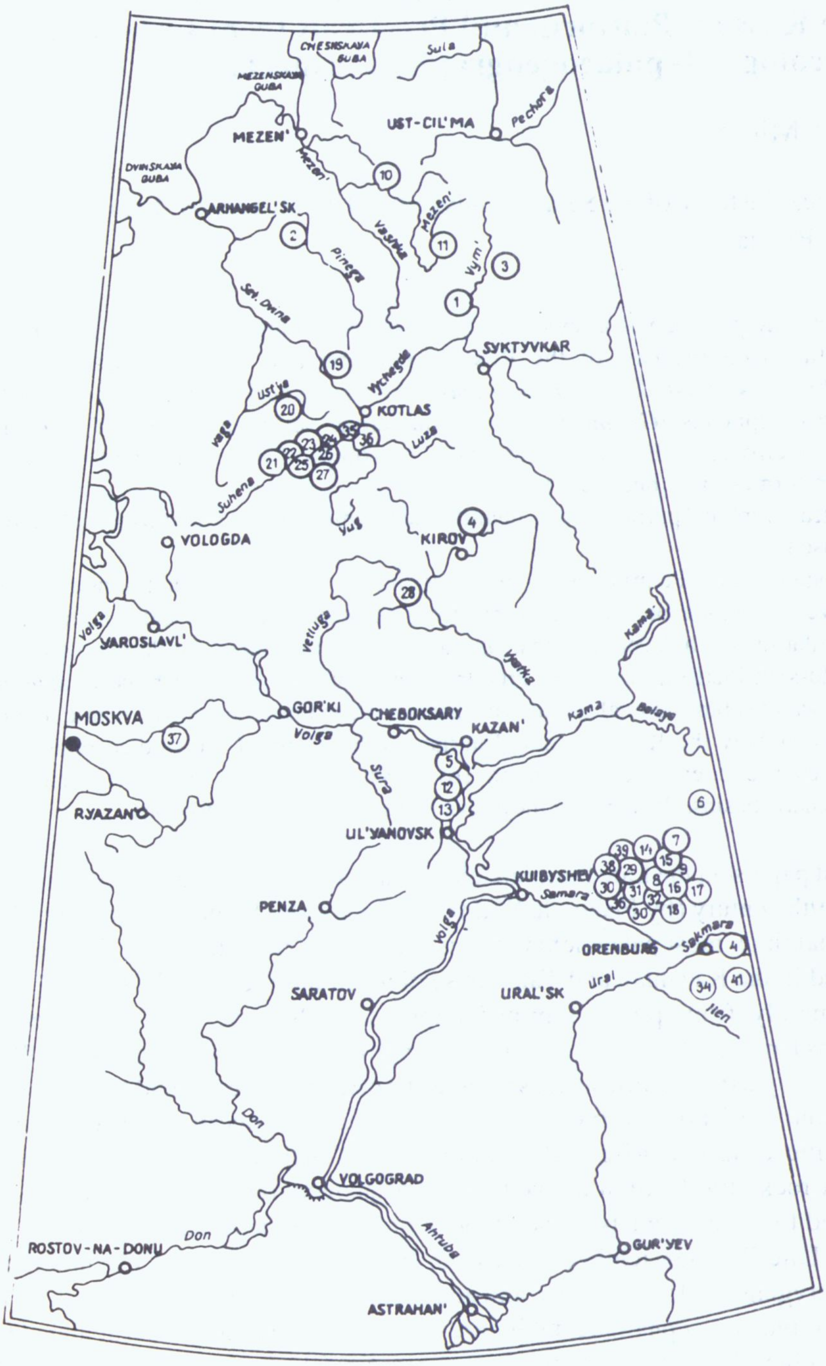
Ecologically Late Permian fishes are rather diverse. Their living conditions and habitats are derived from their skeleton structures, from the associated fauna and from the analogy with similar taxa in adjacent regions. On the whole, at the end of the Permian on the east of the Russian Platform and West Pre-Urals, most of the fishes inhabited a large, often shallow-water submeridional semimarine basin with an unstable hydrodynamic regime.

Taxonomically the Kazanian and Tatarian ichthyofauna of the studied region rather resembles the coeval ichthyofauna from West-European, North-American and South-Asiatic basins. Presumably they have had similar living conditions.

The first papers on the Late Permian ichthyofauna of Russia appeared in the middle of the 19th century (by Fisher de Waldheim, Eichwald, Krotov, Chabakov, Perg). Since that time, most palaeoichthyologists described the articulated fish skeletons collected in the Kazanian and Tatarian sections in the West Pre-Urals at different times mainly from piles of mined cuprous sandstones. Well-preserved fish skeletons have also been found in the stratotype of the Kazanian on the Volga River. Fragmentary fish remains, such as various dermal bones, scales and teeth are found throughout the Upper Permian section on the East European (Russian) Platform and the Pre-Urals (Text-fig. and list of localities). Their usage in practical geology for host rock stratification as well as for palaeogeographic reconstructions was restricted for a long time because of the poor knowledge of the material.

The Late Permian ichthyofauna from this region consists of elasmobranchs, sarcopterygians, holocephalians, and actinopteryians (Table).

Shark and holocephalian remains are usually represented by disarticulated teeth and fin spines, less frequently by skull bones. So, Glückman (1980) has described the early Tatarian ichthyodorulites, teeth, jaws and cranial remains of a large shark *Xenosynechodus egloni* Glükm. from the Early Tatarian Isheyevo vertebrate



Main occurrences of the Late Permian ichthyofauna.
Note: numbers are identical to the ordinal number of occurrences according to the list of the localities.

locality. In Kargala mine we have found some skeletons of small sharks and bradyodonts which are still under study.

Until recently, crossopterygians and dipnoans have not been recorded in the Permian rocks of the USSR. Only lately the author (Minich, 1989) has described a partly worn tooth plate *Gnathorhiza tatarica* Min. from Tatarian Vyatka rocks of the South Pre-Urals. We have also found a fragment of a tooth plate *Gnathorhiza otschevi* Min. from the Tatarian North Dvina Horizon of the Pre-Urals. This dipnoan was previously known only in the Lower Triassic Vetluga Series of the platform. In addition to the redeposited tooth plates of gnathorhizas in the Kazanian and Tatarian rocks, in 1989 the author has found abandoned vertical cylindrical burrows. They had served as shelters for the dipnoans in case of unfavourable conditions of draught or during breeding periods. Similar burrows have been described from the Lower Permian of Kansas, Oklahoma, Michigan and New Mexico (for references see McAllister, 1987; Olson and Bolles, 1975; McAllister, this volume).

Actinopterygians comprise the largest and the most complicated diverse group of the Late Permian ichthyofauna. Their classifyication we is given according to Kazantzeva-Selezneva (1981) with some supplements. The actinopterygians under investigation may be preliminarily divided into five orders: Palaeonisciformes, Elonichthyiformes, Cheirolepiformes, Eurynotoidiformes and Platysomiformes.

The order Palaeonisciformes includes several families, of those the family Palaeoniscidae comprises the type genus *Palaeoniscum* with the species *P. kasanense* Gein. et Vetter, 1880, which is represented by the complete body cast from the Late Kazanian limestones at the village Pechishchi on the Volga River. The genus *Trachelacanthus*, including the species *T. stschurovskii* Fischer, 1851, belongs to the same family. This genus comes from the Ufa Stage of the Vym River basin. Unfortunately, all these and many other type specimens of the fish species described earlier that are kept in several museums of our country are insufficient in numbers for modern morphological studies. Moreover, on account of the strict rules of storage they are not readily available and may be used only as a comparative material.

In the Late Permian ichthyofauna, the order Elonichthyiformes comprises the families Atherstoniidae Gardiner, 1945; Pygopteridae Aldinger, 1937; Acrolepididae Aldinger, 1937; Gonatodidae Gardiner, 1967 and Varialepididae A. Minich (1986). Atherstoniids are represented by *Atherstonia razumovskyi* Chabakov, 1928, described by the cast from the concretion of cuprous sandstone found in Kargala mines near Orenburg. The dubious scales of *Pygopterus* sp. from the Kazanian of the Middle Volga region are provisionally included in Pygopteriids. Within the family Acrolepididae two species of the genus *Acrolepis* Agassiz, 1883 — *A. rhombifera* and *A. macroderma* — have been described by Eichwald (1861) on the basis of the incomplete skeletons found from piles of cuprous sandstones from Kargala. *A. macroderma* ranges practically througnout the Permian, but *A. rhombifera* occurs only in its upper stage. Gonathoidiids are represented by the genus *Toyemia* Min., 1989 (Minich and Minich, A. 1989), with the species *T. tverdochlebovi* Min. having a characteristic scale form and sculpture. This species comes from the Late Tatarian rocks of the Russian Platform. Varialepidiids belong to the genus *Varialepis* A.Min., 1986, including the species *V. bergi* which have been collected in the Early Tatarian rocks of the Orenburg Pre-Urals and in the Middle Volga region.

The order Cheirolepiformes comprises the family Karaunguriidae Kazant.,1977, with the genus *Samarichthys* A.Min., 1989 coming from the Early Tatarian of the Orenburg region (Minich,A., 1986).

The genus *Amblypterina* described by Berg (1940), as a part of the Late Permian ichthyofauna of the Pre-Urals, is, in our opinion, the synonym of the genus *Eurynotoides* Berg, 1940. The specimens, ascribed by Eichwald (1861) and Chabakov (1939) to the genus *Amblypterus* Agassiz, need redescription.

Among the deep-bodied representatives of the order Platysomidae, in the Late Permian ichthyofauna of the Russian Platform, two genera — *Platysomus* Agassiz with the species *P. biarmicus Eichw., 1857 and genus Kargalichthys* (Minich, 1986) with the species *K. efremovi* Min. — belong to the family Platysomidae.

Eichwald's species *Platysomus biarmicus* was re-studied by the author (Minich, 1986) on the basis of some new material consisting of eight almost intact fish skeletons from the Kichkass locality, Kargala mines near Orenburg. As a result, the cranial bone structures, earlier unknown in the species, were distinguished. This allowed us to confirm the idea that the species "*biarmicus*" belonged to the genus *Platysomus* Agassiz. In this connection the paper by Campbell and Phuoc Le Duy (1983) on cranial structures of the type species *Platysomus gibbosus* Ag. was of great help.

Kargalichthys efremovi comes from the same strata as *Platysomus biarmicus* Eichw., but this fish clearly differs from it in the skull structure, dentition and the scale sculpture. The genus *Kargalichthys* contains several species from different horizons of the Kazanian and Tatarian stages of the Russian Platform.

Fishes separated recently by the author and A.Minich (1989) into a new order Eurynotoidiformes (with one family Eurynotoididae) make up a large group in the Late Permian ichthyofauna in the region under consideration. The genus *Eurynotoides* (Berg, 1940) [with the species *E. nanus* (Eichw.), 1860 from Kargala mines is the type genus. Some Early Tatarian genera also belong to the family Eurynotoididae. These are: *Lapkosubia* A.Min.,1989 (with species *L. uranensis* A.Min. and *L. barbalepis* A.Min.) and *Kichkassia* Min., 1989 (with the species *K. furcae* Min.) from the Kichkass locality, and also the Late Tatarian genera *Isadia* A.Min., 1986 (Minich, A. and Minich, 1986), with the species *I. suchonensis* A.Min.,1986 and *I. aristoviensis* A.Min., 1989, collected in the North Dvina and Vyatka horizons in the Sukhona River basin and in the South Pre-Urals. Still, there are many fish specimens not described yet which may improve and supplement our knowledge of the Permian ichthyofauna of the region under consideration.

Some Late Permian fish groups have successfully been used for stratigraphical purposes. Thus the species of the deep-bodied fishes of the genus *Platysomus* differ clearly enough in the Late Kazanian, Early and Late Tatarian. Species of the genera *Eurynotoides*, *Lapkosubia* and *Kichkassia* also differ considerably from the Late Tatarian species of the genus *Isadia*. The latter — *I. suchonensis* and *I. aristoviensis* — date the North Dvina and Vyatka horizons, respectively. The species of the genera *Toyemia* and *Mutovinia* may be considered only as the Late Tatarian ones, whereas the representatives of the genera *Varialepis* and *Samarichthys* are characteristic of the Early Tatarian age.

The ecological aspects of the Late Permian ichthyofauna of the Russian Platform and the Pre-Urals has not been studied in detail yet. There is only one paper by Chabakov (1926-27) in which the author tries to find out the habitat of fishes on the basis of host rock facies. E.g. Chabakov considered the occurrence of deep-bodied forms of the family Platysomidae in clayey and marly rocks of the Tatarian Stage as an evidence of the dwelling of those fishes in stagnant and quiet water. Later Solodukho (1951), having found the same deep-bodied fishes in clayey dolomites of the "podboy" series of the Kazanian Stage, defined the habitat of platysomids as lagoonal-marine.

However, such an identification of the environments of fishes on the basis of the rock facies is not always thorough or convincing enough since burials are rarely autochthonous. Besides, the genetic type of the sediment cannot be always defined indisputably. In practice one has often to judge the conditions of host sediment formation by fossils. For example, the analysis of the ichthyofauna has assisted the establishment of the genesis of the sand lenses of the "North Dvina" type, often occurring in the Permian clayey-carbonate sections of the studied region. Usually such lenses have been considered as alluvial-fluviatile (channel) deposits (Ignatev, 1963, 1966) or channel deposits of deltaic arms (Efremov, 1954; Tverdokhlebov, 1987, 1989) and their occurrence in a section has been ascribed to frequent vertical movements.

However, such common features of sand lenses as ribbon banding vaguely resembling a river bed, erosional incision and gradual covering by fine sediments, frequent graded bedding along with cross bedding, as well as the absence of other facies of alluvial series (floodplain, dead channel type) — all this does not allow us to agree with the previous interpretations.

Besides, in a number of sand lenses (e.g., in Mutovino on the Sukhona River, Aristovo on the North Dvina River and some others), fish remains are to be found similar to those in adjacent basin rocks. This may argue in favour of the formation of such sand bodies in the same water basin as the surrounding clayey and carbonate deposits. In order to explain the frequent occurrence of such a "channel alluvium" in thick basin sediments, it is probably not necessary to refer to intense vertical oscillatory movements. Let us remember the underwater gravity transport of sediment (avalanche sedimentation according to Lisitzin, 1988) from shallow (nearshore) parts to deep parts of the basin by turbidity and suspension currents in the form of the so-called turbidites. These are precisely characterized by ribbon banding, substrate erosion and graded bedding. These processes are widespread in nowadays seas, and it seems reasonable to suggest that there was nothing to prevent them from developing in the past.

Another method for defining the environment of animals is the morpho-functional analysis of their skeletons. The body form, the presence, structure and relation of paired and axial fins, the development and structure of their teeth, the character of squamation, orbit size and the presence of a sclerotic ring in it, etc. are very informative as to the environment of palaeoniscoid fishes. For example, one may evaluate the salinity of a basin on the basis of the presence or absence of additional nostrils in an eye notch where well-developed or reduced tear glands are usually located for removing the excess of salt. On the other hand, it may be useful to refer to an analogous habitat of closely related fishes in other regions where paleosalinity has already been established.

It is necessery to point out that all the late Permian fish species in the studied region for which the skull structure is known, have a well-developed additional pair of nostrils, which implies relatively saline water in their habitation area. This can be confirmed by the presence of two pairs of nostrils in taxonomically close fishes in contemporaneous marine basin of Western Europe (Zechstein) and Eastern Greenland (Aldinger, 1937).

Another important aspect of the study of the Late Permian ichthyofauna in our region is the long-standing problem of the genesis (marine or continental ?) of host rocks. The presence of fish remains in red-bed terrigenous and clayey-carbonate rocks was deemed not to contradict a rather widely accepted assumption about the predominance of the continental sedimentation environment, i.e. lacustrine, lacustrine-deltaic, alluvial, proluvial, eolic, etc. in the Kazanian and Tatarian of the studied region (Ignatev, 1963, 1966; Kuleva, 1980; Tverdokhlebov, 1987, 1989; Forsch, 1963 etc.). Other investigations suggesting the marine genesis of the Tatarian red beds (Tikhvinskaya, 1946), were not taken into consideration.

The main argument for the continental genesis of the Late Permian red beds seems to be the terrestrial and fresh-water character of the main fauna and flora groups buried in them. However, with regard to fishes, such a conclusion is not correct, since there are several forms in the Kazanian and Tatarian fish assemblages that have always been considered to be marine. These are the representatives of the genera *Palaeoniscum* and *Acrolepis* — active marine predators known also in the European Zechstein in cuprous and marly shales, and in the Posidonian shales in the Upper Permian of Eastern Greenland. Almost everywhere they occur together with marine invertebrates (Aldinger, 1937).

The deep-bodied fishes of the family Platysomidae inhabited reefs and stagnant shallow marine lagoons overgrown with algae, and estuaries from the Carboniferous to Triassic. They fed on algae, small crustaceans and molluscs. The occurrence of the Kazanian platysomids in a lagoon-marine basin has been mentioned by Solodukho (1951). Besides the Pre-Urals, these fishes lived in the basins of Western Europe (Campbell, Phuoc Le Duy, 1983) and in South-East Asia and China (Wei Feng, 1977). That may argue in favour of a similar environment as well as probable connection between these marine basins.

In the Kazanian and Tatarian stages of the East European Platform and in the Pre-Urals there occur shark remains of the genus *Wodnika* and bradyodonts of the genus *Janassa* (Chabakov, 1939), which are also known in the marine lagoonal sediments of the Late Permian age in Western Europe.

As already mentioned, in the Middle Volga region in the Tatarian sandy rocks at the village Isheyevo, the remains of rather large sharks have been found, their length reaching about 2.5 m. Certainly such large sharks could not inhabit shallow and temporary water basins which according to the supporters of the continental origin of the red beds (Tverdokhlebov, 1987, etc.), supposedly existed in the region at the end of the Permian. Already Orlov (1968) wrote about the possible deltaic character of the Isheyevo bone-bearing beds and the vicinity of the sea.

Lungfish tooth plate remains known from the Tatarian rocks of the Orenburg region have been subjected to significant transport and redeposition. Recently, the author has also succeeded in finding evidences of abandoned burrows of lungfishes secondarily colonized by crustaceans. This shows that some parts of the basin could have become shallower and even dried up.

On the whole, the analysis of skeletal remains and traces of life activities of elasmobranchs, dipnoans, crossopterygians, and palaeoniscoids shows a wide range of environments in a large recurrent basin with an unstable hydrochemical regime. Wide occurrence of marine ecological groups among the fishes permits us to speak of the existence in the East of the Russian Platform and in the Pre-Urals during the Kazanian and the most of the Tatarian of the extensive epicontinental abnormally marine, gradually extinguishing basin which could have had periodical connection to the open sea. Numerous rivers from the West and the East discharged their waters into this basin, which might have had a jagged shoreline and many islands. These rivers could be determined only by debris transported onshore and into deltas. The debris was periodically transported into the basin by turbidity and suspension currents and formed the first stage of an avalanche sedimentation in the sea (Lisitzin, 1988).

As for ostracodes, conchostracans and bivalves inhabiting such a basin, they could presumably adapt both to much fresher or more brackish water. Their dependence in the past on water salinity has not been studied in detail yet. Many tetrapods have adapted to water environment.

Thus, pareiasaur remains, numerous in the Tatarian which Amalitzky and Sushkin considered to be those of land dwellers, are nowadays thought to be those of swimming seal-like animals feeding on water vegetation. Terrestrial forms of vertebrates, as well as wood from land, might have been transported (according to Efremov) into the basin by rivers.

The present concept of a sufficiently prolonged existence of a large semimarine basin during the Late Permian in the East of the Russian Platform, as confirmed by the ecological analysis of ichthyofauna adaptation, has recently got some other palaeontological evidence. Thus, in the Amanack Formation of the Tatarian of the Orenburg Pre-Urals the rockforming coccolith-like algae have been found. They are perfect indicators of the marine sedimentation environment.

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List of the main Late Permian fish localities on the East of the Russian Platform

Ufa Stage
(P_2uf)

1. River Vym

Kazanian Stage
Lower substage
(P_2kz_1)

2. River Pinega
3. Ust-Koin

Kazanian Stage
Upper substage
(P_2kz_2)

4. Shchovo-Chirky
5. Pechishchi
6. Belebey
7. Saray-Gir
8. Pritokskiy
9. Bolshoy Uren

Tatarian Stage
Lower substage
Urzhum Horizon
(P_2t_1ur)

10. River Mezen
11. Polyany stan
12. Isheyevo
13. Klyuchevskoy ovrag
14. Sadak
15. Outcrop 902
16. Osinki
17. Kargala mines
18. Kichkass

Tatarian Stage
Upper substage
North Dvina Horizon
(P_2t_2sd)

19. Verhnaya Toyma
20. River Ustya
21. Navoloki
22. Opoki
23. Mikulino
24. Mutovino
25. Dmitriyevo
26. Mouth of the Strelnya River
27. Strelnya
28. Site 40
29. Korolki
30. Babintzevo
31. Boyevoy
32. Adamovka
33. Raptanka
34. Donguz VI

Tatarian Stage
Upper substage
Vyatka Horizon
(P_2t_2vt)

35. Salarevo
36. Aristovo
37. Vyazniki
38. Novogorodetzkoye
39. Outcrop 359
40. Vyazovka
41. Blaumenthal III

Table

The occurrence of ichthyofauna in the Late Permian of the Russian Platform

Taxa / Indices	P_2uf	P_2kz_1	P_2kz_2	P_2t_1ur	P_2t_2sd	P_2t_2v
Elasmobranchii						
Xenosynechodus egloni Glük ., 1980			- -	12	- -	
Wodnika invicta A.Min. (in litt.)				- -	- -	37
Holocephali						
Janassa bituminosa (Schlot.)	–	2	5	18	–	
Dipnoi						
Gnathorhiza tatarica Min., 1989				- -	- -	38
G. otschevi Min., 1977			–	—	29	- -
Actinopterygii						
Palaeoniscum kasanense (Gein. et Vetter), 1880		–	5	–		
Atherstonia razumovski Chab., 1928			–	17	–	
Toyemia tverdochlebovi Min., 1989			–	18, 27, 22,	27, 29, 31, 34	41
Varialepis bergi A.Min., 1986			–	13, 18	- -	41 -
Samarichthys luxuria A.Min., 1989			–	18	–	
Eurynotoides nanus (Eichw.), 1860			–	17	–	
E. costatus (Eichw.), 1860			–	17	–	
Lapkosubia uranensis A.Min., 1989			–	18	–	
L. barbalepis A.Min., 1989			–	18	–	
Kichkassia furcae Min., 1989			–	18	–	
Isadia suchonensis A.Min., 1989				–	20-28, 32,	34-35
I. aristoviensis A.Min., 1989					– 32, 36,	39-41
Trachelacantus stschurovski Ficher	1	- -				
Platysomus biarmicus Eichw., 1857			–	10-16, 18	–	
P. bashkiricus Min. (in litt.)		–	7	–		
P. soloduchiensis Min. (in litt.)		– 3,	5, 7, 9	–		
Kargalichthys efremovi Min., 1986			–	14, 18	–	
K. pritokensis Min. (in litt.)		–	8	–		
Mutovinia stella Min. (in litt.)				–	24	39 –

Note : numbers are the same as the ordinal number of occurrences according to the list.

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A

1

FOSSIL FISHES AS LIVING ANIMALS

ACADEMIA

1

FOSSIL FISHES AS LIVING ANIMALS