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A new Lower Devonian arthrodire (Placodermi) from the NW Siberian Platform

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Abstract. A new genus and species of arthrodires, *Eukaia elongata* (Actinolepidoidei, Placodermi), is described from the Lower Devonian, ?Pragian of the Turukhansk region, NW Siberian Platform. A single specimen of the fish, a skull roof, comes probably from the lower part of the Razvedochnyj Formation. The occurrence of an actinolepidoid arthrodire in the Early Devonian of this area of Siberia is unexpected. *Eukaia* shows some distant relationship with the genus *Actinolepis*, but several features indicate similarity to representatives of other arthrodires.

Key words: actinolepidoid arthrodire, placoderm, Lower Devonian, ?Pragian, NW Siberian Platform.

INTRODUCTION

The northwestern part of the Siberian Platform in the Russian Arctic is well known for rich and amphiaspidid-dominated Early Devonian fish faunas. One of the important areas where these faunas have been discovered is the near-Yenisej zone of the Tunguska syneclise (Krylova et al. 1967). The Devonian strata are exposed on the right bank of the Yenisej River, on its tributaries Kulumbe, Kurejka, Severnaya and others. The Devonian occurs also northwards, in the Norilsk region (in drill cores) and in a few exposures (Fig. 1). Numerous fossil fish finds come mainly from the Lochkovian Kurejka Formation (Fm), which has yielded large collections of amphiaspidids – agnathans, specific to the Devonian of Siberia. These heterostracans are less common in the overlying Razvedochnyj Fm, particularly in its lower, Pragian part. Placoderms are found in both formations, but they have so far been mentioned in only lists of fossils or described in rare cases (Mark-Kurik 1994, 2010). In the 1970s and 1980s the present author identified fossil fishes, collected by geologists working in the Norilsk region and near-Yenisej outcrop area. The specimens included a placoderm skull roof, which probably came from the Pragian. A detailed description and reconstruction of this interesting specimen are given in this paper.

GEOLOGICAL SETTING

The Lower Devonian sequence in the Kulumbe-Kurejka and Norilsk regions comprises four formations: the Zub, Kurejka, Razvedochnyj Fms and part of the Mantura Fm (Fig. 1). The first two units are Lochkovian in age, the lower part of the Razvedochnyj Fm belongs to the Pragian and the upper part of the Razvedochnyj Fm plus the lower part of the Mantura Fm to the Emsian (Matukhin 1995). The **Zub** Fm (up to 150 m thick) consists of carbonaceous-argillaceous and sulphate rocks. Invertebrates and fossil fishes, e.g. a cyathaspidid *Steinaspis*, are comparatively rare (Krylova et al. 1967). The **Kurejka** Fm (up to 104 m thick) is represented by grey, green and red argillites and marls. Many amphiaspidids, from more than 10 genera, come from this formation. Of placoderms mainly acanthothoracids have been reported, one of them identified as *Romundina* sp. (Mark-Kurik 1994). The fish assemblage contains also acanthodians, the sarcopterygian *Porolepis kureikensis* (Vorobyeva 1963) and the actinopterygian (palaeoniscoid) *Dialipina markae*, found in the eastern part of the Tunguska syneclise, Kotuj River basin (Schultze 1992). A remark by D. V. Obruchev on the occurrence of Bradyodonti gen. n. in the Kurejka Fm of the same area is of great interest (Obruchev et al. 1973, p. 201). According to Obruchev, the fish, coming from the Lochkovian, is perhaps the earliest bradyodont, i.e., a representative of the Order Bradyodonti, Subclass Holocephali. The bradyodonts are known from the Upper Devonian to the Lower Triassic (Obruchev 1964). It is not excluded that an extraordinary twisted tooth plate from the Lochkovian dark grey limestone of Kotel′nyj Island, New Siberian Archipelago (Mark-Kurik 1975, fig. 1) also belongs to a Devonian holocephalan.

The **Razvedochnyj** Fm (up to 160 m thick) is composed of varicoloured and grey argillites, siltstones and siliceous rocks. Several amphiaspidids, the rhenanid *Dolganosteus remotus* Mark-Kurik, 2010 and undescribed placoderms

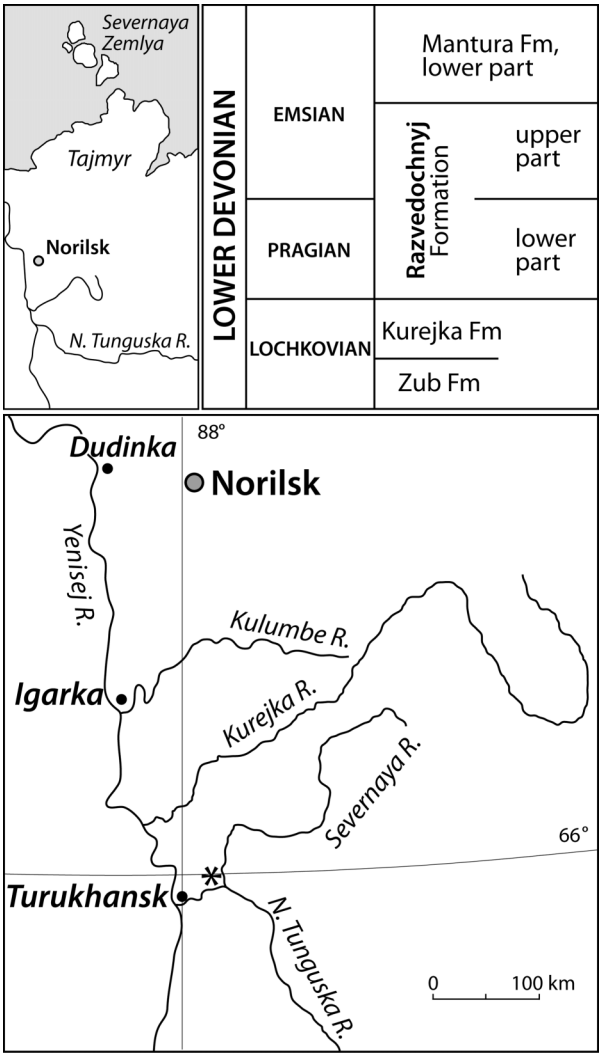

Fig. 1. Sketch maps of northwestern Siberia, Russian Federation; the asterisk * shows the locality of *Eukaia* gen. nov. On the upper right: subdivisions of the Lower Devonian in the NW part of the Siberian Platform.

(e.g. *Norilaspis hamata* Obruchev nomen nudum), acanthodians, *Porolepis* and an actinopterygian (palaeniscoid), different from *Dialipina*, occur in the lower, Pragian part of the formation (Obruchev et al. 1973; Schultze 1992; Matukhin 1995). The upper, Emsian part of the formation contains a quite different fish assemblage, consisting of placoderms – petalichthyid *Wijdeaspis*, buchnosteids, large arthrodires, e.g. the heterosteid *Tollichthys*, and several sarcopterygians. Similar fossil fishes are reported from the lower (upper Emsian) part of the Mantura Fm (Mark-Kurik 1991; Matukhin 1995).

Numerous jawless fishes characteristic of the Siberian Early Devonian, amphiaspidids, come mostly from the Siberian Platform, also from the adjacent Tajmyr Peninsula. These heterostracans have been studied and described thoroughly by L. Novitskaya in a number of monographs and papers (for references see Novitskaya & Afanassieva 2004). The Early Devonian fish assemblages include, besides the dominating amphiaspidids, also cephalaspids, different placoderms, acanthodians, sarcopterygians (porolepiforms) and actinopterygians. However, the representatives of other fish groups are mainly just listed (Obruchev et al. 1973; Mark-Kurik 1994; Matukhin 1995), but described in only a few cases (a rhenanid, a porolepiform and two actinopterygians) as indicated above.

A new arthrodire genus is of note. The type specimen comes from the Severnaya River downstream area in the Turukhansk region, from the most southern outcrops of the Kurejka and Razvedochnyj Fms. Matukhin & Menner (1974, pp. 22, 31) described very briefly the Lower Devonian section in this part of the Severnaya River. The Kurejka Fm is 30–35 m thick. The lower two-thirds of the formation consist mainly of greenish-grey rocks. The upper part has yielded vertebrate remains and gastropods. The overlying Razvedochnyj Fm is about 10 m thick. It consists of metamorphic ferruginous variegated silty-clayey and siliceous rocks. Fish fossils, including amphiaspids (*Gerronaspis* sp., Hibernaspididae), cephalaspids, large arthrodires and sarcopterygians, show that the lowermost part of the Razvedochnyj Fm is exposed. As the rock sample with the skull of the new arthrodire is similar to reddish silty-clayey rocks of the Razvedochnyj Fm, it can be supposed that the specimen probably came from this level.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI M'Coy, 1848
Order ARTHRODIRA Woodward, 1891
Suborder ACTINOLEPIDOIDEI Miles, 1973
Family *incerta sedis*
Genus *Eukaia* Mark-Kurik gen. nov.

Etymology. From the first syllables of the given name and surname of Eugenia P. Kasperkevich, and the Latin suffix *-ia*, denoting 'pertaining to'. She was the geologist who discovered this unique fish specimen.

Type species. *Eukaia elongata* gen. et sp. nov.

Diagnosis. As for the type and only known species.

Eukaia elongata Mark-Kurik gen. et sp. nov.
Figures 2, 3

Etymology. The species name *elongata* means 'prolonged' in Latin, according to the long nuchal plate.

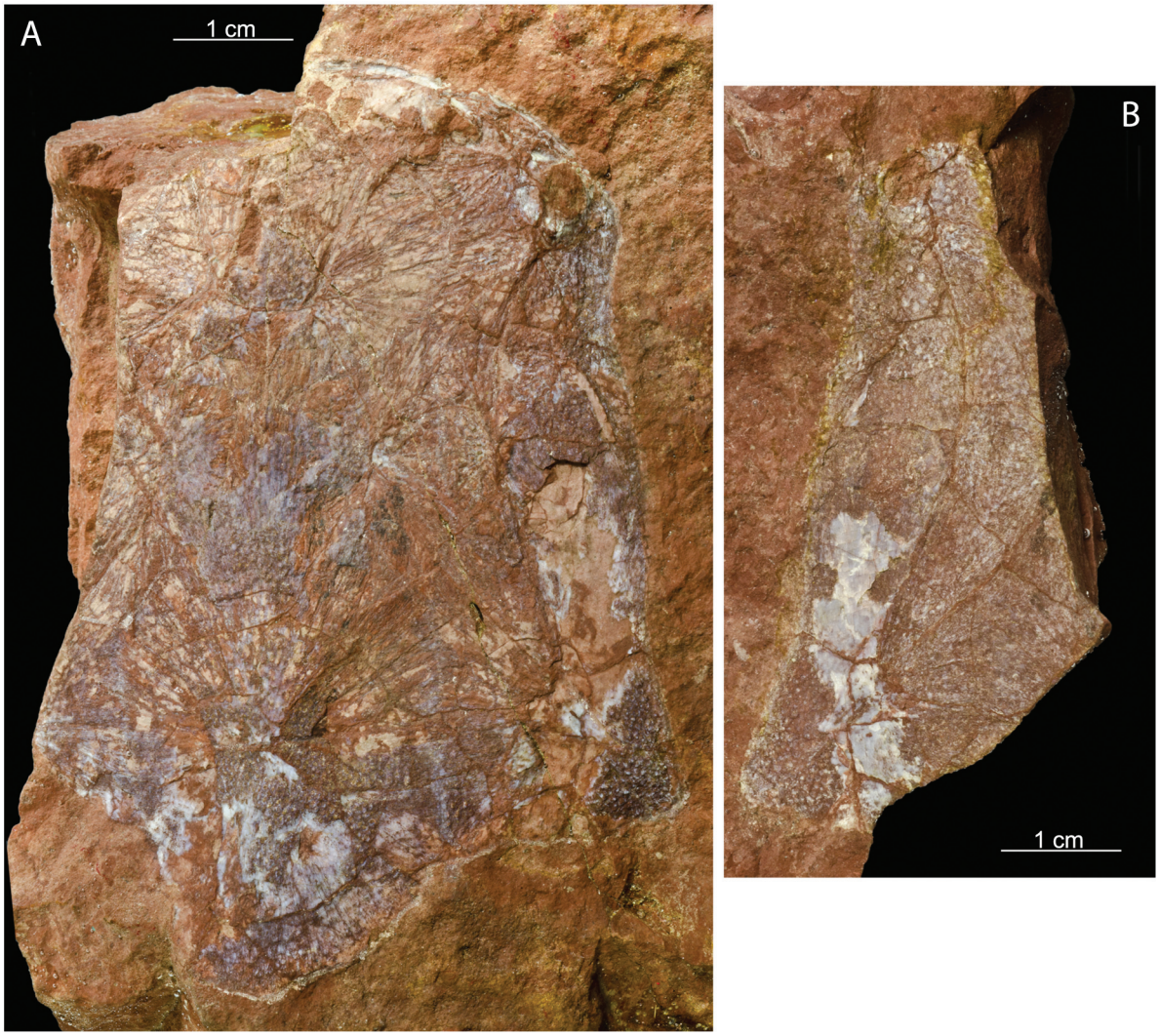

Fig. 2. *Eukaia elongata* gen. et sp. nov. **A**, skull roof, dorsal view (GIT 604-4, holotype); **B**, counterpart of the right side of specimen GIT 604-4. Specimens are photographed under water.

Holotype and the single specimen, GIT 604-4, skull roof (Figs 2, 3).

Locality. NW Siberian Platform, Turukhansk region. The Severnaya River (the right tributary of the Nizhnaya Tunguska River), right bank, 8 km from the river mouth, sample No. 130g, collected in 1973 by E. P. Kasperkevich (VSEGEI).

Horizon and age. E. P. Kasperkevich wrote on the label that the specimen came either from the Kurejka Fm or the lower part of the Razvedochnyj Fm (Members 1, 2). As the reddish-brown silty-clayey rock sample with the skull specimen of *Eukaia* resembles largely the rock of the Razvedochnyj Fm described by Matukhin & Menner (1974, p. 31), it could come from this formation. As the lower part of the Razvedochnyj Fm is of Pragian age (Matukhin 1995), the age of the arthrodire can provisionally be considered as Pragian.

Diagnosis. An actinolepidoid arthrodire of moderate size. The postnasal plates are large. The excurrent nasal openings are on the dorsal side of the skull roof. Small eyes are at the anterolateral corner of the skull roof. The rostral and pineal plates are partly fused. A transverse pit-line joins the supraorbital sensory lines and the ossification centres of partly fused preorbital plates. The postorbital plate is small. The suborbital plate is completely fused to skull roof. The anterior narrow process of the nuchal plate separates the central plates. A very large and long nuchal plate is about two thirds of the length of the skull roof, and reaches further back

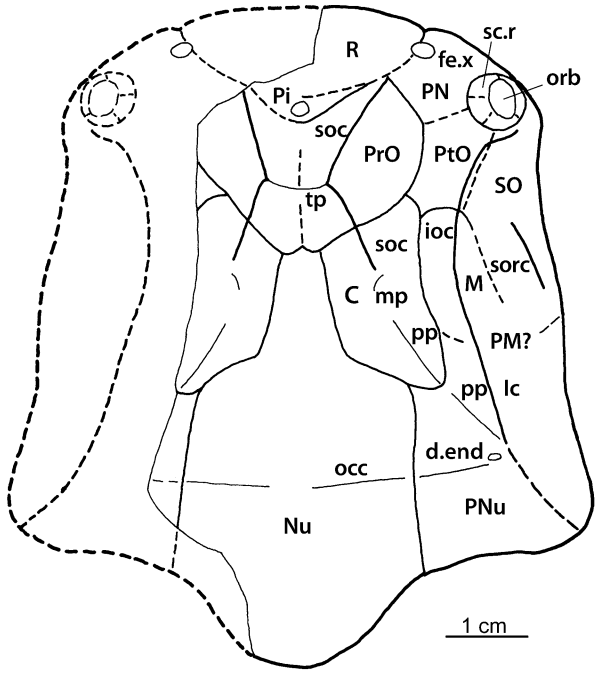

Fig. 3. *Eukaia elongata* gen. et sp. nov. Attempted restoration of the dermal plate pattern in the skull roof. Abbreviations: C, central plate; d.end, foramen of endolymphatic duct; fe.x, excurrent nasal opening; ioc, infraorbital sensory line; lc, main lateral line; M, marginal plate; mp, middle pit-line; Nu, nuchal plate; occ, occipital cross commissure; orb, orbital opening; Pi, pineal plate; PM?, postmarginal? plate; PN, postnasal plate; PNu, paranuchal plate; pp, posterior pit-line; PrO, preorbital plate; PtO, postorbital plate; R, rostral plate; sc.r, sclerotic ring; SO, suborbital plate; soc, supraorbital sensory line; sorc, supraoral sensory line; tp, transverse pit-line.

from the posterior margins of the paranuchal plates. The occipital cross commissures meet at the ossification centre of the nuchal plate.

Description. The skull roof is preserved as a part (Fig. 2A) and a counterpart of the right side of the specimen (Fig. 2B); about one third of its left side is missing. The skull roof is of moderate size, 7.8 cm in length and 5.5 cm in incomplete width in the posterior part of the specimen; when complete, the width could be approximately 6.5 cm. The anterior part is almost flat, the posterior part is slightly convex; the height of the posterior end of the skull is 1.2 cm. The ornament of the specimen is largely missing. A patch of bone is completely destroyed at the posterior portion of the right margin. The posterior edge of the skull roof is irregularly broken, and not complete to some extent. Most of the external surface shows bone trabeculae, which help to trace the outlines of the plates. However, numerous fine cracks complicate this action. Sensory lines and pit-lines are variously preserved; some are not easy to trace, particularly pit-lines. The right eye opening at the anterolateral corner of the skull, surrounded by sclerotic plates, is comparatively well preserved, whereas the nasal opening and especially the foramen of the endolymphatic duct are hardly traceable. The ornament is poorly preserved. There are some patches of tubercles, e.g. at the posterolateral corner of the skull roof. The counterpart (Fig. 2B) shows that irregular or round tubercles of different size covered the skull. The diameter of tubercles is 0.5–0.7 mm.

The skull roof plate pattern of *Eukaia* (Fig. 3) is simple and does not reveal any double plates (e.g. paranuchals) as in acanthothoracids or petalichthyids. The anterior margin of the skull slopes gently downwards. There is a large but very poorly preserved rostral plate (R); only its general shape can be estimated. It is roughly triangular with a moderately convex anterior margin, and when restored, twice as wide as long. In its posterior portion the R plate is partly? fused with a narrow pineal plate (Pi) that lies in a shallow embayment formed of the anterior margins of the preorbital plates (PrO). The Pi plate is evidenced by a protuberance, lacking bone and a couple of millimetres in diameter. The plate had probably its own ossification centre. The paired PrO plates appear to form one unit but still have two ossification centres, connected with a transverse pit-line (tp). Both PrO plates have a supraorbital sensory line (soc) that runs anterolaterally from the ossification centres. The sensory line passes also back onto the central plate (C).

A very large and long nuchal plate (Nu) starts from a notch between posterior ends of the PrO plates. The length of the Nu plate is about two thirds of the length of the skull roof. The plate is roughly hexagonal; its anterior end is developed as a slender process between the C plates. The posterior margin is strongly convex and reaches much further back from the posterolateral corners of the paranuchal plates (PNu). The anterior process of the Nu plate separates irregularly-shaped central plates (C). The plates have traces of the middle pit-lines (mp) close at the end of the supraorbital sensory lines, and also posterolaterally directed posterior pit-lines (pp), which continue on the paranuchal plates. The poorly preserved PNu plate is roughly quadrangular with an anteromesial notch for the posterior end of the C plate. The contact with the M plate is not clear. One more ossification centre existed probably between the PNu and M plates; it could indicate the presence of a postmarginal plate (PM?). The main lateral line (lc), the posterior pit-line (pp) and the occipital cross commissure (occ) converge at the centre of the PNu plate. An oval? foramen of the endolymphatic duct is probably present in the PNu plate. Laterally of the right C plate an

ossification centre shows the presence of a small and nearly oval marginal plate (M). The main lateral line (lc) crosses its posterior part and the infraorbital sensory line (ifc) its anterior one.

Three plates surround a slightly oval orbital opening (orb), which is 6.5 mm long. Poorly preserved, probably four thin sclerotic plates surround the small eye opening. Behind the orbital opening is a slender plate, which can be identified as the suborbital plate (SO). A short segment of the infraorbital sensory line occurs close to the orbital opening. One more sensory line in the posterior part of the SO plate, directed backwards from the ossification centre, can be identified as the supraoral sensory line (sorc). The postorbital plate (PtO) in front of the M plate is small and the infraorbital sensory line is situated at its lateral margin. The postnasal plate (PN) is rather large and irregular in shape. Close to its anterior end in contact with the R plate is a poorly preserved excurrent nasal opening (fe.x), about 35 mm long. The PN and SO plates meet at the anterolateral edge of the orbital opening.

Comparison and discussion. The *Eukaia* skull roof plate pattern is simple, resembling that of actinolepidoids, such as *Baringaspis* (Miles 1973) and *Actinolepis* (Mark-Kurik 1973), but the anterior part of the skull roof is only slightly narrower than the posterior part. It is significant that *Eukaia* has no dermal nasal capsule consisting of the R, Pi and PN plates, as known in many actinolepidoids: *Kujdanowiaspis* (Stensiö 1945), *Erikaspis* (Dupret et al. 2007), *Eskimaspis* (Dineley & Liu 1984), *Simblaspis* (Denison 1958) and others. The presence of a very large PN plate in *Eukaia* is of note. A large PN plate is also known in *Bryantolepis* (Denison 1958, 1978). In *Actinolepis* the PN plates are wide but short and border the PrO and PtO plates anteriorly (Mark-Kurik 1973). An especially large PN plate is known in the rhenanid *Brindabellaspis* (Young 1980). The excurrent nasal openings (fe.x) lie in the anterior part of the border between the PN and R plates. The dorsal position of the nasal opening differentiates *Eukaia* from *Bryantolepis* (Denison 1978) and *Lehmanosteus* (Goujet 1984). In these arthrodires the anterior edge of the skull is turned down and nasal openings are faced forwards.

The R plate is poorly preserved. It is a rather large plate as in *Actinolepis* but shorter and wider; the R and Pi plates seem to be fused only partly. As in *Bollandaspis* (Schmidt 1976, fig. 3A), the Pi plate lies in a shallow embayment formed of the anterior margins of the PrO plates, and probably had its own ossification centre, marked with a protuberance. Similarly to the *Actinolepis* species (Mark-Kurik 1973) and *Coccosteus cuspidatus* (Miles & Westoll 1968, text-fig. 9e, f) there is no pineal opening. The PrO plates are not so completely fused as in *Actinolepis* (Mark-Kurik 1973) or *Bollandaspis* (Schmidt 1976). They possess distinct ossification centres in the posterior part of the plates as e.g. in *Lehmanosteus* (Goujet 1984, fig. 110). A transverse pit-line, not known in other arthrodires, joins the centres of the PrO plates. Rare transverse pit-line may occur in some other placoderms. One of them is described in the petalichthyid *Eurycaraspis*; it is marked as the second posterior pit-line (pp_2) and joins the centres of the anterior PNu plates (Liu 1991). In *Actinolepis* the supraorbital sensory lines meet at the common ossification centre of the PrO plates, which is not the case in *Bollandaspis* and *Eukaia*.

As in *Actinolepis*, in *Eukaia* the paired PrO plates do not reach the orbital openings and have a more central position. However, the PtO plate is much smaller than the same plate in *Actinolepis*. In many actinolepidoids and phlyctaenioids the PtO plate is rather large, bounding the orbital opening from behind. Sensory lines branch off from its ossification centre (Denison 1958, fig. 105), but this is not the case in *Eukaia*, which lacks the central sensory line (csc). In *Eukaia* the supraorbital sensory lines (soc) cross from the PrO plates to the C plates. The position of the supraorbital sensory line is similar to that of *Holonema* (Miles 1971, fig. 4) and not known in actinolepidoids. The C plates have the middle pit-lines (mp) and posterior pit-lines (pp); the latter pass towards the ossification centre of the PNu plate. A narrow anterior process of the Nu plate separates the central plates. In *Baringaspis* (Miles 1973, fig. 2) the C plates are separated in the same way.

The Nu plate is remarkably large and extends further back than the PNu plates. This is unusual for actinolepidoids. The situation is somewhat similar in phlyctaenioids, e.g. in *Groenlandaspis* (Young & Goujet 2003, fig. 26C). However, the occipital cross commissures (occ) continue in *Eukaia* almost to the middle of the Nu plate as in *Actinolepis* (Mark-Kurik 1973, text-fig. 1A). The general outline and position of the Nu plate resemble those of *Baringaspis* (Miles 1973, fig. 2), although the plate is much wider. A well-preserved main lateral line (lc) passes from the C plate to the ossification centre of the PNu plate, where it nearly meets both the posterior pit-line and occipital cross commisure. The latter is much longer than in many other actinolepidoids, but resembles the condition in *Actinolepis*. An elongated SO plate forms the anterolateral part of the skull roof. This plate is firmly fused with the skull roof, which is not common in actinolepidoids. A close contact of the SO plate with the R and PtO plates exists in the brachythoracid *Holonema* (Miles 1971). In *Eukaia* the infraorbital sensory line (ioc) is developed on the SO plate as a short segment near the orbital opening, whereas in *Holonema* it crosses the entire SO

plate (Miles 1971, figs 32, 33). *Eukaia* has the supraoral sensory line (sorc) in the posterior part of the SO plate. The supraoral sensory line is comparatively rare in arthodires, including actinolepidoids (Denison 1958). It has been identified in *Holonema* (Miles 1971, fig. 32) and *Buchanosteus* (Mark-Kurik 2004, figs 4, 5).

Three plates, PN, PtO and SO, surround the orbital opening. It is significant that the narrow anterior end of the SO plate and the posterolateral process of the PN plate meet one another at the orbital opening. The SO plate is usually not firmly fused to the adjacent skull roof plates in actinolepidoids. It is specific to *Eukaia* that the nasal opening is situated dorsally. In the actinolepidoid *Lehmanosteus* it is faced anteriorly in the downward turned margin of the skull roof (Goujet 1984, fig. 112). *Bryantolepis* has also a similar structure of the nasal opening and a rather large PN plate (Denison 1978, fig. 34).

The eye opening of *Eukaia* is comparatively small; its length is 4.5 mm. It is surrounded by a poorly preserved thin sclerotic ring with a maximal width of 2 mm in its mesial part. As the ring is cracked in several places, it is hard to establish how many plates it consists of; their number is probably four. The plates vary in size. The external surface of the sclerotic ring is ornamented. The number of sclerotic plates varies largely in placoderms. In rhenanids these plates are especially numerous, e.g. ten in *Gemuendina* (Janvier 1998, fig. 4.55A). Arthrodires have commonly four sclerotic plates, e.g. *Dicksonosteus* (Goujet 1984, fig. 19), *Coccosteus* (Miles & Westoll 1968, text-fig. 9) and *Holonema* (Miles 1971, fig. 37). However, five plates have been identified in various placoderms, e.g. in the homostiid *Goodradigbeeon* (White 1978, fig. 53) and acanthothoracid *Murrindalaspis* (Long & Young 1988, fig. 3A), but there one of the plates does not reach the eye opening. In the acanthothoracid *Romundina* cf. *stellina* four sclerotic plates surround a fairly large and round eye opening (Goujet & Young 2004, fig. 3C). Antiarchs possess three sclerotic plates, e.g. *Yunnanolepis* (Zhang 1980, fig. 1a), *Asterolepis* (Lukševičs 2001, fig. 6) and *Bothriolepis* (Stensiö 1948, fig. 30). Another aspect is also significant: the sclerotic plates may be either thin as probably in *Eukaia*, also in the large and specific arthrodire *Carolowilhelmina* (Mark-Kurik & Carls 2002, fig. 16) or thick as in *Holonema* (Miles 1971, fig. 37).

CONCLUSIONS

Classifying the arthrodire *Eukaia* is difficult as only the skull roof of the fish has been found. Therefore important characters in the structure of its neck joint and trunk shield cannot be considered. The genus is established based on rather large postnasal plates, the position of the excurrent nasal openings on the dorsal side of the skull roof, small eyes at the anterolateral corner of the skull, the suborbital plate that is completely fused to the skull roof and the very large nuchal plate. The partly fused rostral and pineal plates, also partly fused preorbital plates and the presence of long occipital cross commissures on the nuchal and paranuchal plates show some similarity between *Eukaia* and such actinolepidoids as *Actinolepis* and *Bollandaspis*. A number of features have been used to join these genera into the family Actinolepididae (Dupret et al. 2009, fig. 3) or a distinct group among 'actinolepids' (Dupret 2004). Twenty-eight characters of the skull roof of the Arthrodira, listed by Dupret et al. (2009, Appendix 2), can be compared in *Eukaia* and *Actinolepis tuberculata*; 22 of them coincide and six are different in these species. Also, the rostral and pineal plates, and postorbital plates are not completely fused into one plate in *Eukaia*. These characters foreshadow the complete fusion of the plates in *Bollandaspis* and *Actinolepis*. However, some characters of *Eukaia*: small postorbital plate and the suborbital plate, firmly fused to the skull roof, and a very large nuchal plate, which is considerably longer than the paranuchals and has a strongly convex posterior margin, separate the new genus from this group and indicate its relationship with other arthrodires.

Bollandaspis and *Actinolepis* come from the Emsian and Eifelian/Givetian (Johnson et al. 2000, fig. 9) of Europe – Belgium, Baltic area and Scotland (Newman & Trewin 2008). The age dating of the earliest representative of *Actinolepis* (*A. spinosa*) has changed; the level where the species comes from is probably Emsian (Karatajūtė-Talimaa 1997). Interestingly, *Eukaia* with its probable early Pragian age seems to indicate a distant relationship with arthrodire genera from quite different regions and fish assemblages. However, the occurrence of *Actinolepis* sp. in the Eifelian Vstrechnaya Formation of Severnaya Zemlya (Mark-Kurik 1991, p. 15) shows that the distribution of Early/Middle Devonian fish faunas was wider than believed so far. A discovery of an actinolepidoid arthrodire from the northwest of the Siberian Platform is an important addition to the Early Devonian fish fauna of this area.

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Uus Alam-Devoni artrodiir (Placodermi) Siberi platvormi loodeosast

Elga Mark-Kurik

On kirjeldatud uut artrodiiri (plakodermide ehk rüükalade) perekonda ja liiki *Eukaia elongata*. Selle kala koljukaas leiti Siberist Jenissei jõgikonnast Severnaja jõe suudme lähedalt Turuhanski piirkonnast. Kihid, mis sisaldasid *Eukaia* koljut, kuuluvad tõenäoliselt Alam-Devoni vanusega Razvedotšnõi kihistu alumisse ossa, seega Praha ladejärku. Aktinolepidoidide alamseltsi kuuluva artrodiiri leid Siberi platvormi loodeosast on üllatav. *Eukaia* näib suguluses olevat perekond *Actinolepis*'e liikidega, keda on leitud nii Euroopa Vara- ja Kesk-Devonist kui ka Severnaja Zemlja Kesk-Devonist. Kuid sellel kalal esineb tunnuseid, mida leidub ka teistesse rühmadesse kuuluvatel artrodiiridel.