Elgaecrinus uralicus gen. et sp. nov., a new crotalocrinitid (Crinoidea, Echinodermata) from the Lower Devonian (Lochkovian) of the Middle Urals

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Abstract. *Elgaecrinus uralicus* gen. et sp. nov. (Crotalocrinitidae, Crinoidea, Echinodermata), a reef-dwelling crinoid, is described from the Lochkovian (Lower Devonian) of the western slope of the Middle Urals. The arms of the new species are laterally fused in each radius and represent, as in the similar genus *Crotalocrinites*, uniform semi-mobile plates surrounding the central cavity above the oral surface in an en echelon series. This crown architecture allowed for feeding in rapidly changing turbulent currents characteristic of the reef zone.

Key words: Crinoidea, Early Devonian, Urals, morphology, ecology, functional-morphological analysis.

INTRODUCTION

The European periphery of the Uralian Ocean (southern part of the vast Paleoasiatic Ocean) in the Silurian and Devonian was likely a centre of origin and distribution for many groups of benthic organisms. Despite commonly incomplete preservation, fossils from the Silurian and Devonian deposits of the Western Urals are popular subjects for palaeontological study due to their high taxonomic diversity and abundance, resulting from the variety of habitats and palaeogeography of the basin. Joint fieldwork was conducted in the Urals in 1973 with a group of Estonian palaeontologists led by Elga Mark-Kurik and the field team of A. Zhivkovich, to study the fossil fish and crinoids of Silurian and Devonian deposits of the Ufimian Amphitheatre. Through this joint work, I was able to find an interesting crinoid locality near the waterline in the middle reaches of the Serga River, which contained diverse crinoid cups, stems and other remains of these animals. To collect supplementary material, I revisited this locality in 1978. As a result, the locality yielded a representative collection of Early Devonian crinoids (cups, pluricolumnals, columnals and other separate ossicles), even though some were incompletely preserved. I described three species and two genera of pisocrinids (Rozhnov 1981) from this locality and also reported the occurrence of loboliths and cups of Scyphocrinites ex gr. excavatus (Schl.), indicating that the host deposits fall within the Silurian-Devonian boundary interval. Records of the

conodont Icriodus woschmidti allowed these beds to be dated more precisely as the Lochkovian (Early Devonian) (Zhivkovich & Chekhovich 1985). Other crinoids from this locality have remained undescribed until now. Among these, two cups belonged to a new species of Crotalocrinitidae, a family common in the Silurian and Early Devonian. Crotalocrinitids have previously been reported from the Urals (Yakovlev 1949; Arendt & Hecker 1960), but the new find is particularly interesting, as the new genus and species described from these cups represents a taxon possibly ancestral to Crotalocrinites, whereas crotalocrinitids are the earliest but highly specialized among known Gasterocomoidea (Webster 2012). In 2006, these two cups were the subject of the MSc thesis of V. G. Malkov, my MSc student in the Department of Paleontology of the Geological Faculty of Moscow State University. Unfortunately he did not continue the study of these fossils. Results of the fieldwork were later discussed with Elga Mark-Kurik when we met in Tallinn. I named the new crotalocrinitid genus described in this paper after Elga to commemorate our joint fieldwork in the Urals.

MATERIAL AND METHODS

This paper is based on two cups from a locality on the right bank of the Serga River 8 km south of the town of Nizhnie Sergi, 500 m south of the Katnikova Cave (Fig. 1). The specimens studied come from a packstone

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Fig. 1. Map of the locality.

bed cropping out near the waterline of the Serga River, with a high content (60%) of crinoid stem fragments. This bed represents the base of a series of 15 thin gradational members separated by beds of dark calcareous clay shale. The total thickness of the member is 2.8 m. It is overlain by a uniform series almost completely composed of dark, thin-bedded micritic limestones, 5-6 m thick (Zhivkovich & Chekhovich 1985). Conodonts (Icriodus woschmidti) found in this series indicate the Lochkovian Stage of the Lower Devonian (Zhivkovich & Chekhovich 1985). The bed of bioclastic argillaceous limestone sedimentologically represents fore-reef proximal carbonate debris (Zhivkovich & Chekhovich 1985). Apart from the crinoids described in the paper, the same bed contained the cups of Eucalyptocrinites sp., Lecanocrinus sp., Geroldicrinus sp., Pisocrinus (Pocillocrinus) concinnus Rozhnov, Pisocrinus (Granulosocrinus) bohemicus Bouška, Parapisocrinus ollula grandis (Bouška), loboliths and cups of Scyphocrinites ex gr. excavatus (Schl.), diverse crinoid columnals, and also jointed brachials of uncertain taxonomic affinity.

The collection studied is housed in the Borissiak Paleontological Institute, Russian Academy of Sciences, No. PIN3424.

SYSTEMATIC PALAEONTOLOGY

Class CRINOIDEA Subclass CLADIDA Order CYATHOCRININA Superfamily GASTEROCOMOIDEA Family CROTALOCRINITIDAE Bassler, 1938 Genus *Elgaecrinus* gen. nov.

Type species. Elgaecrinus uralicus sp. nov., Lower Devonian of the Ufimian Amphitheatre.

Diagnosis. Cup small, conical, smooth, with wide facet for stem attachment. Infrabasal circlet of five identical plates; visible in lateral view of cup. Basal circlet composed of largest plates. CD interray basal support narrow anal X plate with rounded distal notch facing cup axis. It interrupts the radial circlet of five plates. Radial plates low, with wide facets, concave and inclined outwards. Each facet penetrated in the centre by a wide canal. Axillary primibrachial small, in the facet centre entirely or almost entirely covered by two axillary secundibrachials, almost entirely occupying facet of radials. Secundibrachials of adjacent radii are separated by rising edges of arm facets or projecting anal plate. Overlying brachials not contacting radials. Stem attachment facet with a wide axial canal.

Composition. Monotypic genus.

Comparison. The new genus is distinguished from the most similar genus Crotalocrinites by the conical rather than rounded cup, smooth rather than prominently ornamented cup surface, auxiliary secundibrachials completely separating tertibrachials from radials. It differs from Enallocrinus in the higher cup with higher basals and radials, in the small rather than wide primibrachial axillary plate, which in the latter genus occupies almost the entire surface of the radial facet. It is different from Achradocrinus in the conical rather than rounded cup, wider radial facets that are inclined rather than subvertical, in the larger anal plate, different plating of the anal opening, and the broad rather than narrow axial canal of the stem facet. It is different from Arachnocrinus in the conical rather than rounded cup, five infrabasals, rather than single fused conical infrabasal circlet, the presence of an anal plate in the cup, in the axillary primibrachials and secundibrachials contacting the radial facet, completely different arm construction and in the rounded rather than square outline of the stem facet, with a wide axial canal with no additional canals. It is distinguished from *Syndetocrinus* by the higher cup and higher infrabasals, the considerably smaller auxiliary primibrachial and different organization of arm branching and the higher basals, the different cup shape and by the clear separation of the cup from the arms. *Elgaecrinus* differs from Parapernerocrinus in the rigidly defined number of the plates in the cup and a different arm branching, and from *Pernerocrinus* in a considerably smaller size, the absence of a thick layer of stereom covering the stem, cup and the proximal crown, and also in a different initial arm branching.

Remarks. Webster (2012) considers that *Crotalocrinites* bashkiricus described by Yakovlev (1949) from the Lower Devonian of Bashkortostan represents a new

genus, intermediate between *Crotalocrinites* and *Pernerocrinus*. *Elgaecrinus uralicus* sp. nov., which comes from almost coeval beds in the same region, is more likely to be ancestral to *Crotalocrinites*.

Occurrence. Lower Devonian, western slope of the Middle Urals.

Elgaecrinus uralicus sp. nov.

Etymology. After Elga Mark-Kurik.

Holotype. PIN, specimen No. 3424/274, south slope of the West Urals, right bank of the Serga River, 8 km south of the town of Nizhnie Sergi. Lower Devonian, Melnichnaya Regional Stage, Katnikov Beds, Lochkovian Stage.

Material. Two well-preserved cups from the Lochkovian (Lower Devonian, Melnichnaya Regional Stage, Katnikov Beds) of the Ufimian Amphitheatre.

Description (Figs 2, 3). Cup small, 5–7 mm, shaped as an upturned truncate cone with an apical angle of \sim 50°, slightly inclined towards the interray BC. The lateral surface is smooth, with no ornamentation. The stem attachment facet is smooth with a wide axial canal, with a diameter ca 2/3 of the facet diameter. The maximum diameter is at the level of the arm attachment facets and 1.5 times as large as the base diameter, and only slightly higher than the cup height. The dimensions of the cups are presented in Table 1.

Five infrabasals similar in size and shape are visible on the side of the cup, 1–2 mm high. The basal circlet has five 2.5–3.5 mm high plates. The CD interray basal plate is flattened distally, supporting the anal X plate, interrupting the radial circlet.

The radial circlet is composed of five similar plates with sharply inclined outwards, concave arm attachment facets narrowing towards the centre of the cup. The highly rising edges of the adjacent radial plates separate the secundibrachials of the adjacent radii. In the interray CD they are separated by the elevated distal part of the anal plate. The height of the radials (without arm attachment facets) is 2–3 mm. The facets are up to 2.5 mm high, around 1.5 mm wide and extend to approximately 0.75 mm towards the cup centre. There is a large opening of the axial canal in the centre of the each facet.

A narrow axillary primibrachial lies in the centre of the facet. Its lateral surface is only slightly visible on the side of the cup. It is distally covered by two axillary secundibrachials occupying the entire width of the facet and adjacent to the rising edges of the radials. Other brachials are not preserved. The opening of the axial canal on the axillary plates is only about half the diameter of the axial canal on the radials.

DISCUSSION

The deposits, in which the cups were found, were formed as a debris flows flanking a reef. Burial occurred at a shallow water (10–20 m depths), as some (mainly bioclastic) beds in the member possess ripple marks. The preservation state of the crinoid remains suggests fast burial near the living site, in a high-energy environment. This is supported by the morphology of most crinoids inhabiting this site, for example, the possession of a strong cup with a reinforced stem attachment, and with arms housed in specialized projections, as in *Eucalyptocrinites*, or the massive cups of pisocrinids with strong arms.

The genus *Elgaecrinus* described herein was adapted, like all crotalocrinitids, to high-energy environments with unstable currents. The main feature of most crotalocrinitids, and primarily of the genus *Crotalocrinus*, which is the most similar to *Elgaecrinus*, is densely packed branches of isotomously branching arms and their fusion by transverse beams in each radius. As a result, the arms in *Crotalocrinites* and, judging from the

Specimen No.	Maximum diameter	Height (without of the arm facets)	Height (with the arm facets)	Stem facet diameter	Axial canal diameter
3424/273	8.1	5.2	7.6	5.2	3.2
3424/274	10.2	6.9	9.6	6.3	4.8
(holotype)					

Table 1. Dimensions of the cups in mm

Fig. 2. *Elgaecrinus uralicus* sp. nov.: **A–H**, holotype PIN3424/274; A–F, lateral view (A, interray AB; B, interray BC; C, interray CD; D, ray D; E, interray DE; F, interray EA), G, top view, H, bottom view; **I–O**, paratype PIN3424/273; I–M, lateral view (I, interray AB; J, interray BC; K, interray CD; L, interray DE; M, interray EA), N, top view, O, bottom view.





Fig. 3. Line drawings showing the arrangement of plates in *Elgaecrinus uralicus* sp. nov: **A**, **B**, paratype PIN3424/273, lateral view (A, ray A; B, interray DE); **C**, **D**, holotype PIN3424/274 (C, ray E; D, interray CD). Infrabasals, basals and facets of radials are white, radials are black, anals are stipped and brachials are grey.

preserved proximal brachials, the arms of *Elgaecrinus* represent in each radius continuous porous non-mobile chevron-like plates. Brett (1984) called the system of crotalocrinitid arms a fine-meshed filtration fan and compared its appearance and possible functions to those of the zoarium of fenestellid bryozoans. He suggested that crotalocrinitid arms functioned as a filtration-feeding baffle. Breimer (1978) suggested that for crotalocrinitid feeding the arms could create ciliary feeding currents through this shield. This assumption seems to be unconvincing, since the water current in the food groove is a by-product of the beating of the cilia to move the food lumps to the mouth. Nutritional particles are caught by ambulacral tentacles located along the entire length of the ambulacrum. Therefore, the water flow in the feeding grooves had no direct functional significance for the catching of food. Perhaps, in the low hydrodynamic waters, the cilia beating could create a weak inflow of water to the crown from the environment. But the crotalocrinitids lived in reef conditions of increased hydrodynamics, and, as is assumed here, the structure of their crown provided a favourable hydrodynamic regime for catching food particles inside the cavity of the crown, formed by the fused branches of the arms. It appears that the rigid, en echelon shields formed by

jointed arm branches are an adaptation to strengthening the crown and gathering food in highly variable, strong currents in a shallow reef or bioherm environment. Indeed, most modern crinoids are passive suspension feeders (Fell 1966). Modern crinoids, e.g., stalkless comatulids or stalked isocrinids, spread their arms while feeding as a flat or parabolic filter fan oriented perpendicularly to the prevailing currents and with the ambulacral grooves directed down-current (Meyer 1979). The tube feet capture nutrient particles by adhesion to mucus covered tube-feet and transfer nutrient lumps enveloped in mucus to the food-gathering groove, in which the ciliate epithelium conveys them to the mouth. Such crinoids are referred to as reophilic, as they are adapted to feeding in even slow currents. In low-energy environments, some crinoids direct their fan of spread arms and the oral surface upwards capturing the descending particles. These are referred to as the reophobic crinoids (Meyer 1973).

Judging from their dense package of brachials, crotalocrinitids could not form such a fan. Arm branches are fused in every radius and are formed of rounded porous plates arranged in an echelon curtain surrounding the central cavity (Fig. 4). Crotalocrinitids lived in highenergy environments with unstable and variable currents,



Fig. 4. Life position reconstruction of *Elgaecrinus uralicus*.

a setting characteristic of very mobile water moving in varying directions, characteristic of the reef and bioherm conditions. These water currents could penetrate the central cavity between the en echelon arms and pores on all sides forming eddies, from which nutrient particles were captured by mucous tube feet. Not only the food-gathering apparatus of crotalocrinaceans, but also the wider stem characteristic of *Elgaecrinus*, judging from the stem facet with attachment structures known from crotalocrinitids, including a wide web of creeping radicular cirri ending in terminal pads of stereomatic secretion (Lowenstam 1957), were adaptions to life in such habitats.

CONCLUSIONS

The morphology of *Elgaecrinus* shows a series of special adaptations to a particular mode of life characteristic of the Late Silurian and Early Devonian. For Crotalocrinitidae, including the new taxon, this is represented primarily by the development of en echelon arm plates, an adaptation to a high-energy environment with

varying current direction. The specialized projections for housing the arms and deeply depressed stem in *Eucalyptocrinites*, and jointed arm plates of unclear taxonomic affinity may also reflect adaptation to rough water environments. Cups and lobolithes (specialized distal part of the stem) of *Scyphocrinites* show adaptations to the temporal anchoring or to a possible pelagic lifestyle and environment. All these crinoids characteristic of the Late Silurian and Early Devonian are found together in a single site on the Serga River alongside *Elgaecrinus* in the debris flow deposits near a fore-reef slope, which was also the source of the *Scyphocrinites* remains which were here mixed with the macrobenthic reophilic fauna. Quite likely *Scyphocrinites* was also a member of this community.

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Elgaecrinus uralicus gen. et sp. nov., uus crotalocrinitiid (Crinoidea, Echinodermata) Kesk-Uurali Alam-Devoni Lochkovi lademest

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Kirjeldatud uus okasnahksete perekond ja liik *Elgaecrinus uralicus* (Crotalocrinitidae, Crinoidea, Echinodermata) on leitud Lochkovi lademe riffmoodustistest Kesk-Uurali läänenõlval. Uue liigi isenditel on haarmed külgmiselt liitunud, moodustades ešelone ümber suuava nagu morfoloogiliselt sarnasel *Crotalocrinites*'el. Selline pähiku ehitus soodustab toidu püüdmist rififaatsiese väga liikuvas vees.