

Coelacanths (Actinistia, Sarcopterygii) from the Famennian (Upper Devonian) of the Holy Cross Mountains, Poland

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ABSTRACT:

SZREK, P. 2007. Coelacanths (Actinistia, Sarcopterygii) from the Famennian (Upper Devonian) of the Holy Cross Mountains, Poland. *Acta Geologica Polonica*, 57 (4), 403-413. Warszawa.

Coelacanth fishes from the Upper Devonian of the Holy Cross Mountains, Poland, are described. The material consists of isolated incomplete lower jaws, gular plates, an entopterygoid and urohyal. The isolated lower jaws belong to *Diplocercides kayseri* (VON KOENEN, 1895). The other coelacanth remains are referred to *Diplocercides* sp. indet. All specimens are Famennian in age (Early *Palmatolepis rhomboidea* conodont Zone), representing a time when almost all of the Holy Cross Mountains carbonate platform was drowned. Because of the shallow-water living conditions preferred by the group it is assumed that these coelacanths were restricted to isolated, small submarine swells, which still existed in that region in the latest Devonian, and that their carcasses were then subjected to *post-mortem* transport into the deeper areas.

Key words: Actinistia, Coelacanths, Late Devonian, Famennian, Holy Cross Mountains, Palaeoenvironment.

INTRODUCTION

The Actinistia (or coelacanths) is a group of sarcopterygian fishes with a long evolutionary history. The oldest coelacanths are known from the Early Devonian (FRIEDMAN & COATES 2006, JOHANSON & al. 2006) but rich sarcopterygian faunas are known from the Middle Devonian (LONG 1999, FOREY & al. 2000). At present, coelacanths are represented only by the emblematic genus *Latimeria*.

Many Late Devonian marine vertebrates such as placoderms (e.g., GÜRICH 1896, GORIZDRO-KULCZYCKA 1934, KULCZYCKI 1957, IVANOV &

GINTER 1997, SZREK 2004), sharks (e.g., GINTER 1990, GINTER & IVANOV 1992), a few porolepids and actinopterygians (KULCZYCKI 1957, LISZKOWSKI & RACKI 1993) and dipnoan fish (GORIZDRO-KULCZYCKA 1950), have been described from the Holy Cross Mountains for more than one hundred years. The coelacanths have not yet been described albeit GORIZDRO-KULCZYCKA (1934, 1950) mentioned *Diplocercides* sp. from the Middle Devonian (*sic.*) of the Tudorów Quarry near Opatów (60 km E of Kielce) and *Diplocercides kayseri* (VON KOENEN) from the Frasnian zone II (*sensu* CZARNOCKI 1947) of the Wietrznia quarry, in the

town of Kielce. There are no descriptions or illustrations in her article and the specimens have been lost. Coelacanth remains from the Holy Cross Mountains have recently been found in a few collections (the Museum of the Earth of the Polish Academy of Sciences, Warsaw, and the Geological Museum of the Holy Cross Mountains Branch of the Polish Geological Institute, Kielce), where they were usually identified as plants or left simply as unidentified fish remains.

The present paper is the first description of Devonian coelacanths from Poland. All of the

specimens described are preserved in shales and come from the Kadzielnia and Wietrznia quarries, now in the southern part of the town of Kielce (Text-fig. 1).

GEOLOGICAL AND PALEOGEOGRAPHICAL SETTINGS

The source localities are located in the in the western part of the Holy Cross Mountains (about 190 km S of Warsaw), in a chain of hills, known as

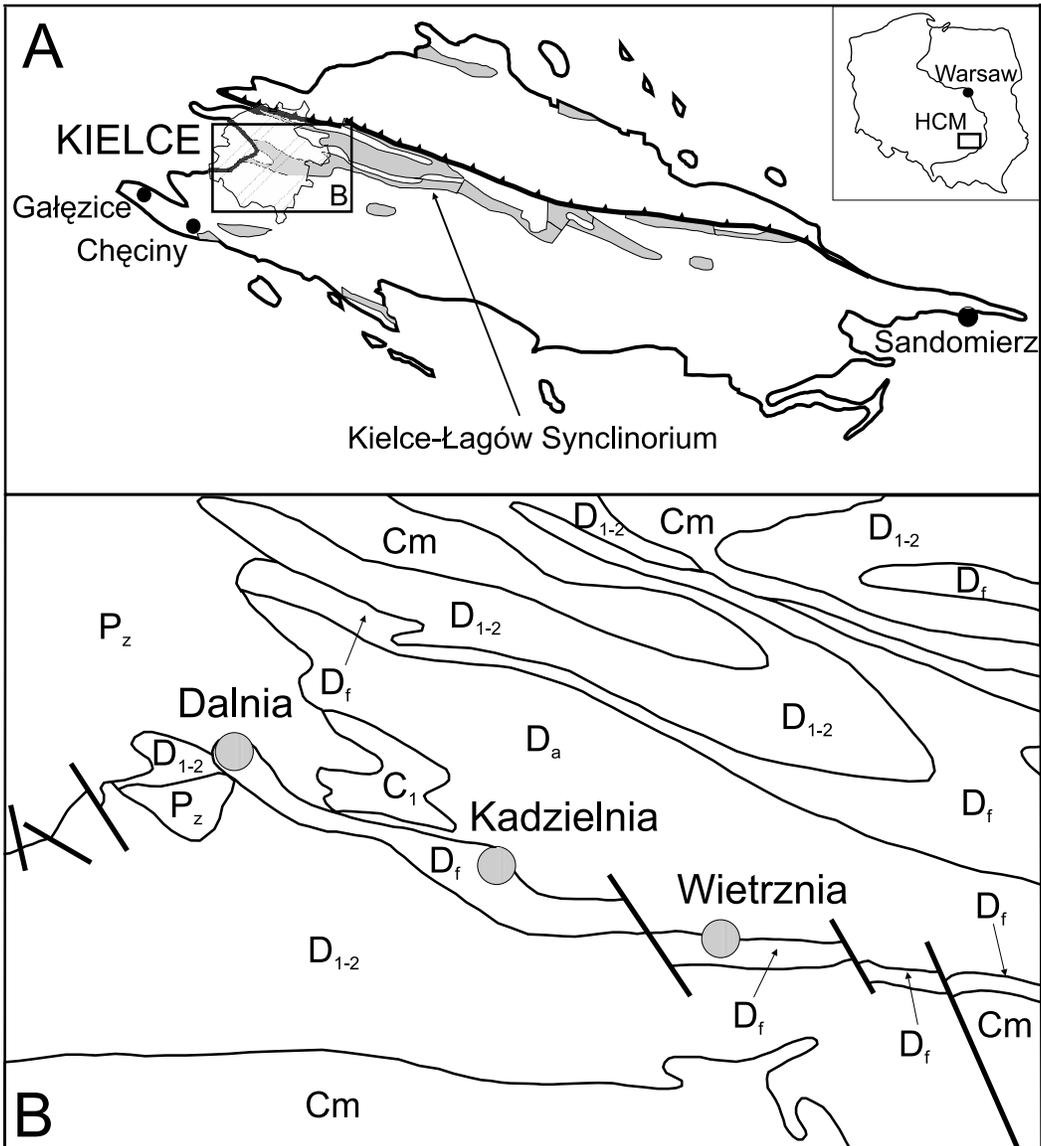


Fig. 1. A – Upper Devonian in the Holy Cross Mountains (after CZARNOCKI 1938, simplified) (grey coloured). B – Geological sketch-map of the western part of the Holy Cross Mountains (Kielce area); Cm + O + S – Cambrian, Ordovician and Silurian, D_{1-2} – Lower and Middle Devonian, D_f – Frasnian, D_a – Famennian, P_z – Permian (Zechstein); HCM – Holy Cross Mountains

the Kadzielnia Range. The range is built of Upper Devonian rocks and belongs structurally to the western part of the Kielce-Łagów Synclinorium (Text-fig. 1).

The Late Devonian facies evolution of the area of the present-day Kadzielnia range is still under discussion. Synsedimentary block tectonics resulted in a wide variety of marine environments in this small area, mainly during the Frasnian (SZULCZEWSKI 1971). In the Late Frasnian the carbonate platform was fragmented and sedimentation over most of the area became uniform, with the deposition of marls, marly shales and shales, except for in isolated places such as Gałęzice (SZULCZEWSKI 1971 and 1995, SZULCZEWSKI & ŻAKOWA 1976 and BEŁKA & SKOMPSKI 1988) or Dalnia (SZULCZEWSKI 1971, 1973 and 1995) (Text-figs 1, 8 and 9). The Famennian succession, expressed as marls and shales, shows progressive stepwise submersion of the carbonate platform.

The boundary between the Famennian shale series and the underlying carbonate deposits is diachronous (SZULCZEWSKI 1971, SZULCZEWSKI & *al.* 1996), being located in the Middle *Palmatolepis crepida* conodont Zone in the Wietrznia Quarry and in the Early *Palmatolepis rhomboidea* conodont Zone at Kadzielnia (SZULCZEWSKI 1989, 1995). This diachronism is due to different subsidence rates of particular blocks as well as facies differentiation and stratigraphic and non depositional gaps. (SZULCZEWSKI 1971).

Of all the samples containing coelacanth remains only those from Kadzielnia yielded well preserved conodonts. This conodont assemblage indicates the Early *Palmatolepis rhomboidea* Zone, corresponding to the lower part of the Famennian succession in this area. Unfortunately conodonts were not found in the Wietrznia samples. Since the oldest Famennian shales in the latter quarry are of Middle *Palmatolepis crepida* Zone age and this series extends up only to the Late *Palmatolepis crepida* conodont Zone, it follows that the age of the coelacanth remains from Wietrznia must fall within this zonal range (Text-fig. 8).

ABBREVIATIONS

Cra – median crest, De – dentary, Gu – gular, Op – operculum, Pt – entopterygoid, msc – mandibular sensory canal, o.Gu – overlap area for

the gular, ang – angular, Spl – splenial, E – early, M – middle, L – late, Lt – latest.

MATERIAL

The available material consists of an association of remains of one individual (a pair of gular plates, a pair of angular plates, an operculum and entopterygoid), two isolated incomplete lower jaws, an entopterygoid, a pair of gular plates, a urohyal, and a few unidentified dermal bones. Some specimens in the collection are not illustrated in the present paper due to the poor state of preservation; only the jaws, urohyal, entopterygoid and gulars were suitable for description. The remains are preserved in shales. Preparation was made with a needle.

The specimens are housed in the following institutions: Museum of the Earth, Polish Academy of Sciences (abbreviated MZ) in Warsaw, Poland and the Geological Museum of the Holy Cross Mountains Branch of the Polish Geological Institute (abbreviated OS) in Kielce, Poland.

SYSTEMATIC PART

Class Osteichthyes HUXLEY, 1880
Subclass Sarcopterygii ROMER, 1955
Infraclass Actinistia COPE, 1871
Genus *Diplocercides* STENSJÖ, 1922

TYPE SPECIES: *Holoptychius kayseri* VON KOENEN, 1895.

Diplocercides kayseri (VON KOENEN, 1895)
(Text-figs 2-5)

1895. *Holoptychius kayseri* n. sp.; VON KOENEN, p. 28;
1937. *Diplocercides kayseri* (VON KOENEN); STENSJÖ,
pp. 36-40, pl. 1-5, pl. 9, fig. 1.

MATERIAL: Six specimens: MZ VIII Vp-373, MZ VIII Vp-383, MZ VIII Vp-384, and MZ VIII Vp-385 (middle Famennian, Kadzielnia Quarry in Kielce); OS-224-36 and OS-224-37 (early Famennian, Wietrznia Quarry in Kielce).

DESCRIPTION: Specimens MZ VIII Vp-383 (Text-fig. 2) and MZ VIII Vp-384 (Text-fig. 3)

show isolated incomplete lower jaws in lateral view. These elements provide almost all the diagnostic features of *Diplocercides kayseri* (VON KOENEN, 1895), a Devonian coelacanth from Germany (STENSIÖ 1937, text-figs 7, 18; pls 1, 3).

MZ VIII Vp-383 (Text-fig. 2) is the anterior part of a right lower jaw with a distinct angular, dentary and splenial. The fragment is large (31.5 mm long) compared to the known *Diplocercides* lower jaws. It shows some details such as a large overlap surface for the gular plate, and a mandibular sensory canal which extends almost diagonally from the

anteroventral part of the angular to its posteromedian or posterodorsal part.

MZ VIII Vp-384 (Text-fig. 3) is smaller than the specimen described above, the total length being 21 mm. The dorsal margin of the angular is gently curved. It differs from the previous specimen in the alignment of mandibular pore-canal which runs along the overlap area for the gular. A short and deep pit-line is present on the splenial. The alignment of the mandibular pit-line is definitely diagonal in the anterior part only. It runs longitudinally in the posterior part.

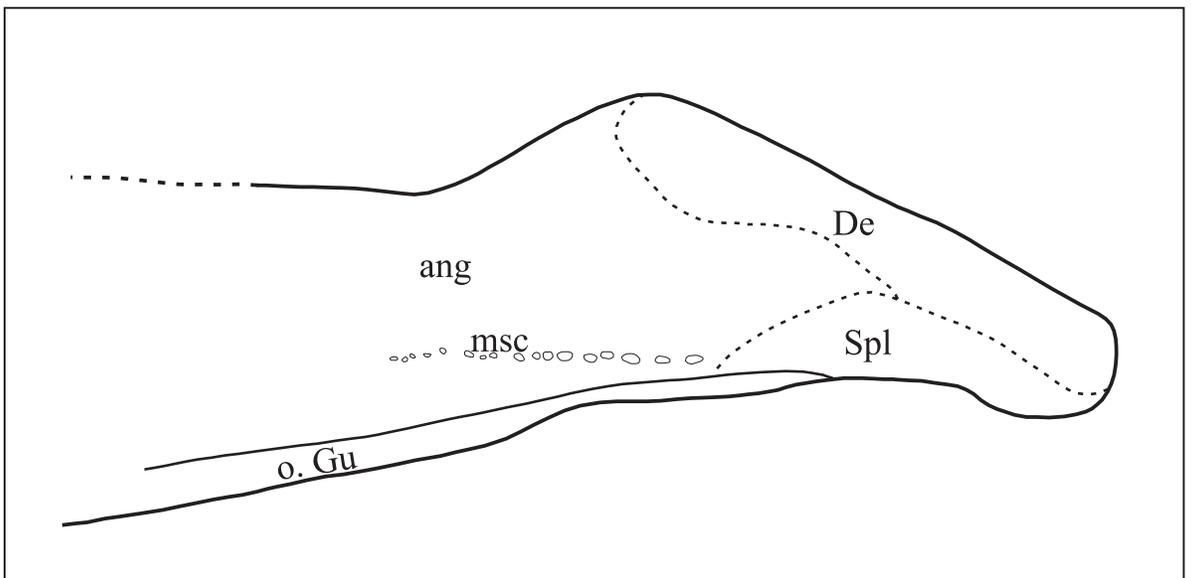


Fig. 2. *Diplocercides kayseri* (VON KOENEN, 1895), MZ VIII Vp-383; Kadzielnia Quarry, Kielce; Anterior part of lower jaw. De – dentary, msc – mandibular sensory canal, o.Gu – surface overlapped with gular plate, ang – angular plate, Spl – splenial plate

Variations in the pattern of the mandibular pit-line in the genus *Diplocercides* were described by JANVIER & MARTIN (1979).

Both specimens are ornamented by rostro-caudal undulating ridges, except on the dentary and the antero-dorsal part of the angular, where the ornament consists of elongated tubercles.

The poorly preserved specimens OS-224-36 and OS-224-37, which are imprints of small parts of the central area of angulars, can be attributed to *Diplocercides* on the basis of this characteristic ornament.

Left and right gular plates were found (specimen MZ VIII Vp-373) on the same piece of rock (Text-fig. 4). Both of them are of the same size (41 mm long and 9 mm wide), so it is very likely that these bones belonged to the same individual. The right gular plate (Text-fig. 4A) is partly destroyed and only the posterior part shows some features

such as ornament and the posterior margin. The lateral margin of the left gular presents a gentle curvature in contrast to the straight medial margin in contact with the other gular plate. The ornament of the anterior part consists of concentric long ridges more or less parallel to the outline of the gular. In the posterior part the ornament consists of long, continuous ridges. All these features were presented by STENSIÖ (1937) and identification of the specimen MZ VIII Vp-373 as *Diplocercides kayseri* (VON KOENEN, 1895) was based on STENSIÖ's descriptions and illustrations.

MZ VIII Vp-385 (Text-fig. 5) represents a left entopterygoid. It is 27 mm long and 16 mm high but these are not exact measurements because the bone is partly destroyed. The element is visible in its lateral aspect, but the dentition on the medial side is visible as impressions in the places where the original bone was damaged. On the basis of other incomplete

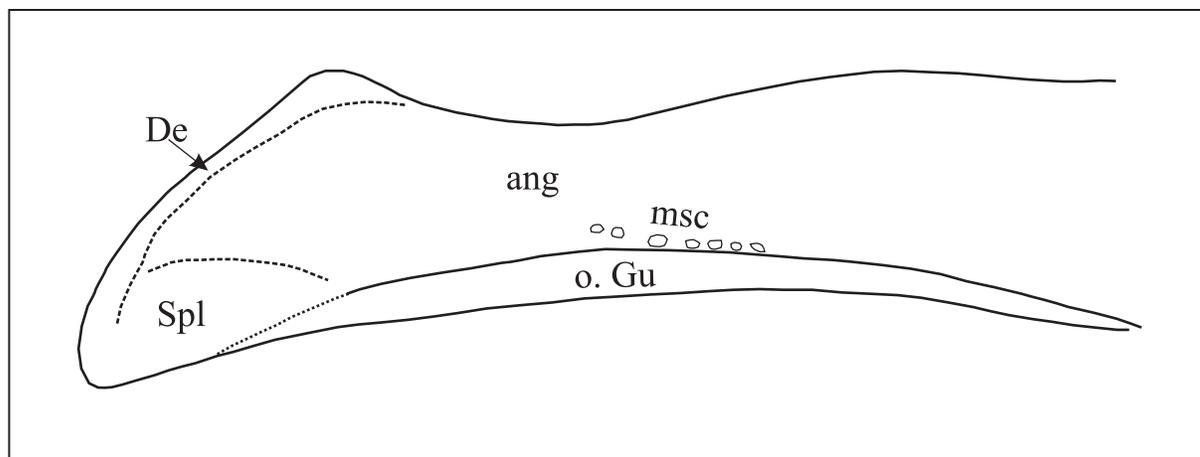


Fig. 3. *Diplocercides kayseri* (VON KOENEN, 1895), MZ VIII Vp-384, Kadzielnia Quarry, Kielce; Anterior part of lower jaw. De – dentary, msc – mandibular sensory canal, o.Gu – surface overlapped with gular plate, ang – angular plate, Spl – splenial plate

entopterygoids from the same locality, it appears that the ornament consists of concentric ridges more or less parallel to the margin in the dorsal region and of small tubercles in the centre of the bone. Shape, size and ornamentation of these entopterygoids are very similar to those seen in *Diplocercides kayseri* (see STENSIÖ 1937, text-fig. 6A, B).

OCCURRENCE: The studied specimens are from the middle Famennian (Early *Palmatolepis rhomboidea* conodont Zone) of the Kadzielnia Quarry, Kielce, and from the early Famennian (Middle *Palmatolepis crepida* to Late *Palmatolepis crepida* Zone) of the Wietrznia Quarry, Kielce.

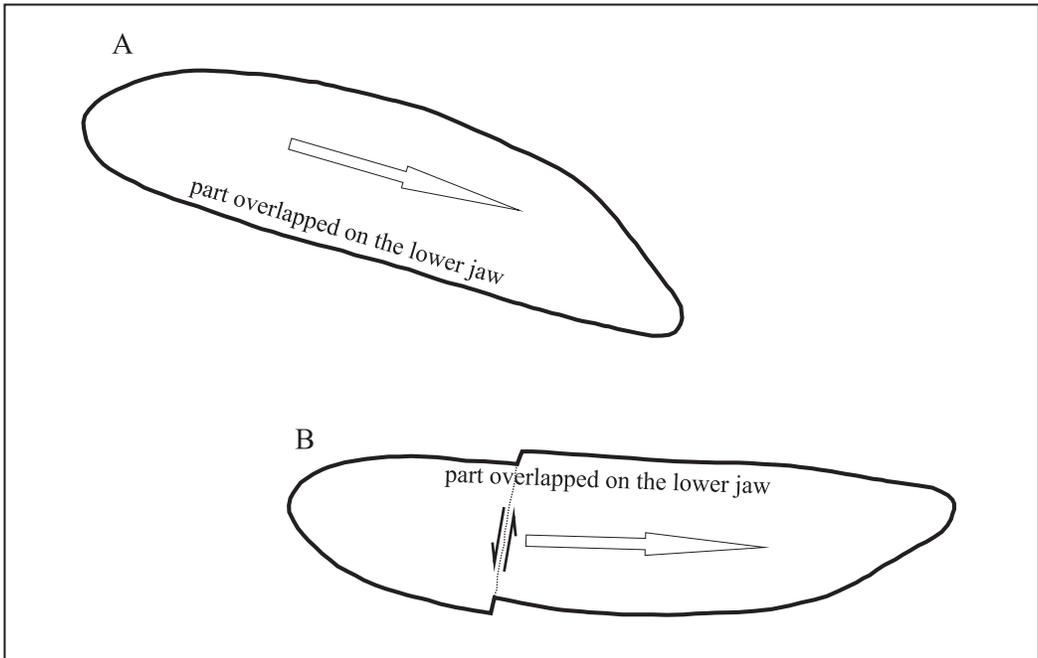


Fig. 4. *Diplocercides kayseri* (VON KOENEN, 1895), MZ VIII Vp-373, Kadzielnia Quarry, Kielce; A pair of gulars; A – left gular, B – right gular. White arrows show forehead

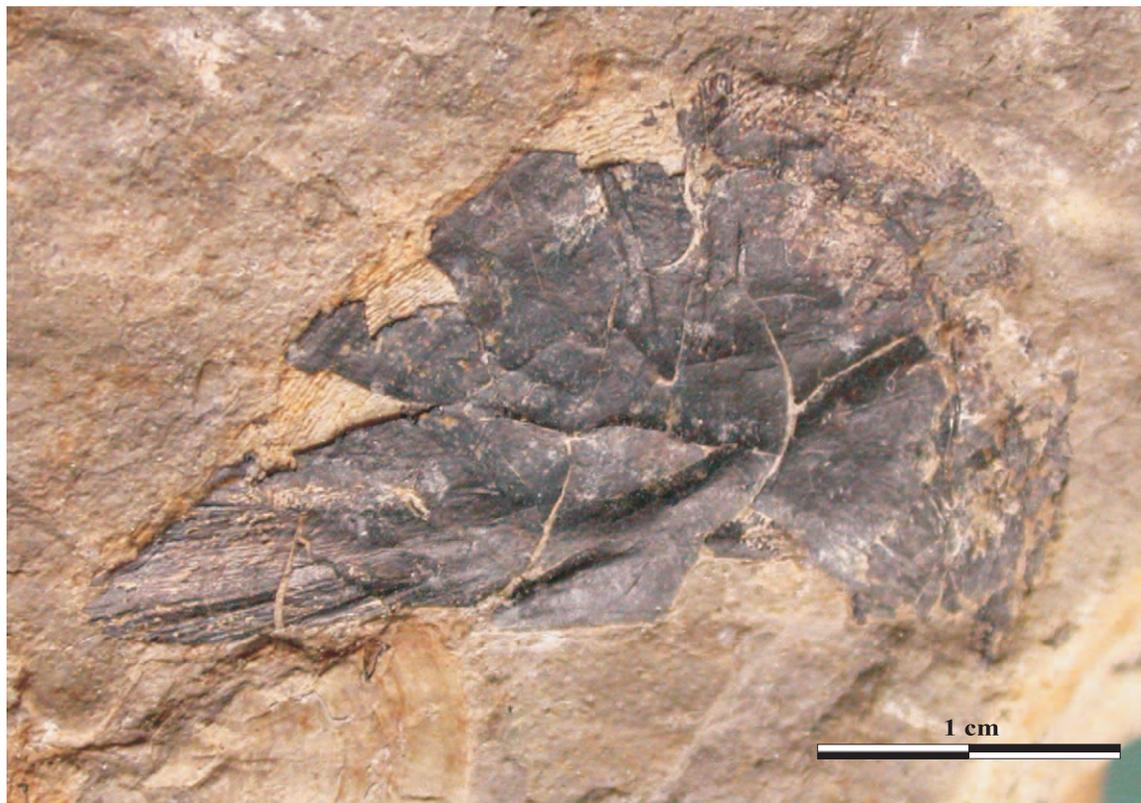


Fig. 5. *Diplocercides kayseri* (VON KOENEN, 1895), MZ VIII Vp-385, Kadzielnia Quarry, Kielce; left entopterygoid

Diplocercides sp. indet.
(Text-figs 6-7)

MATERIAL: Two specimens: MZ VIII Vp-382 (Text-fig. 6) and MZ VIII Vp-386 (Text-fig. 7).

DESCRIPTION: MZ VIII Vp-382 (Text-fig. 6) represents an isolated urohyal, i.e., the median endoskeletal element of the sub-branchial apparatus.

The poor preservation of the specimen makes it impossible to observe any important features except the whole outline and the anterior median crest. It is flattened and no three-dimensional features are visible.

It is quite narrow, fork-shaped posteriorly, and relatively short (total length is 30 mm). The median part of the bone is slender (about 2 mm in width) compared to the twice larger anterior part and the enlarged bifurcated posterior part.

It is similar in overall shape and size to the urohyal of *Nesides schmidti* STENSIÖ, 1937 illustrated by JARVIK (1954, fig. 10B); however, the specimen from the Kadzielnia Quarry seems slightly wider in

its median part and less massive in its bifurcated part. The urohyal in *Diplocercides kayseri* (STENSIÖ 1937, pl. 1) differs from the described specimen in the possession of a wider posterior part (fork-like) and a massive outline. The Famennian coelacanths from the Witpoort Formation, South Africa, considered as close to *Diplocercides* (ANDERSON & *al.* 1994; GESS & HILLER 1995; ANDERSON & *al.* 1999), have urohyals with a wider posterior part, with a rounded outline. The urohyal of an undetermined Famennian actinistian from Morocco is slender throughout its length, with a pronounced median ridge anterior to the bifurcation on its dorsal side (LELIÈVRE & JANVIER 1988). An incomplete urohyal has been found recently amongst other coelacanth remains, in the Late Devonian of Chahriseh, Iran (V. HAIRAPETIAN, personal communication). This latter urohyal has the usual bifurcated shape but looks more massive and robust than the urohyal described herein. All these differences in the shape of the urohyal in these specimens could be caused by different states of preservation. The other Late Devonian coelacanths do not provide any information on the urohyal. It is difficult to identify a

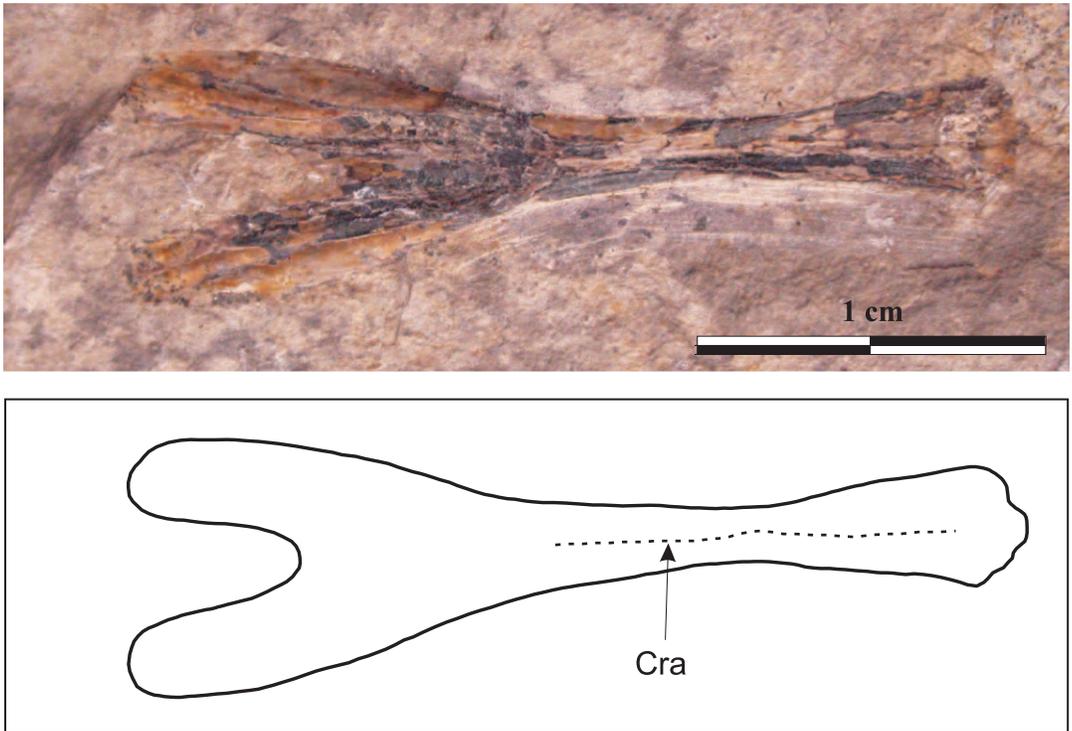


Fig. 6. *Diplocercides* sp., MZ VIII Vp-382, Kadzielnia Quarry, Kielce; Sublingual bone – urohyal. Cra – median crest

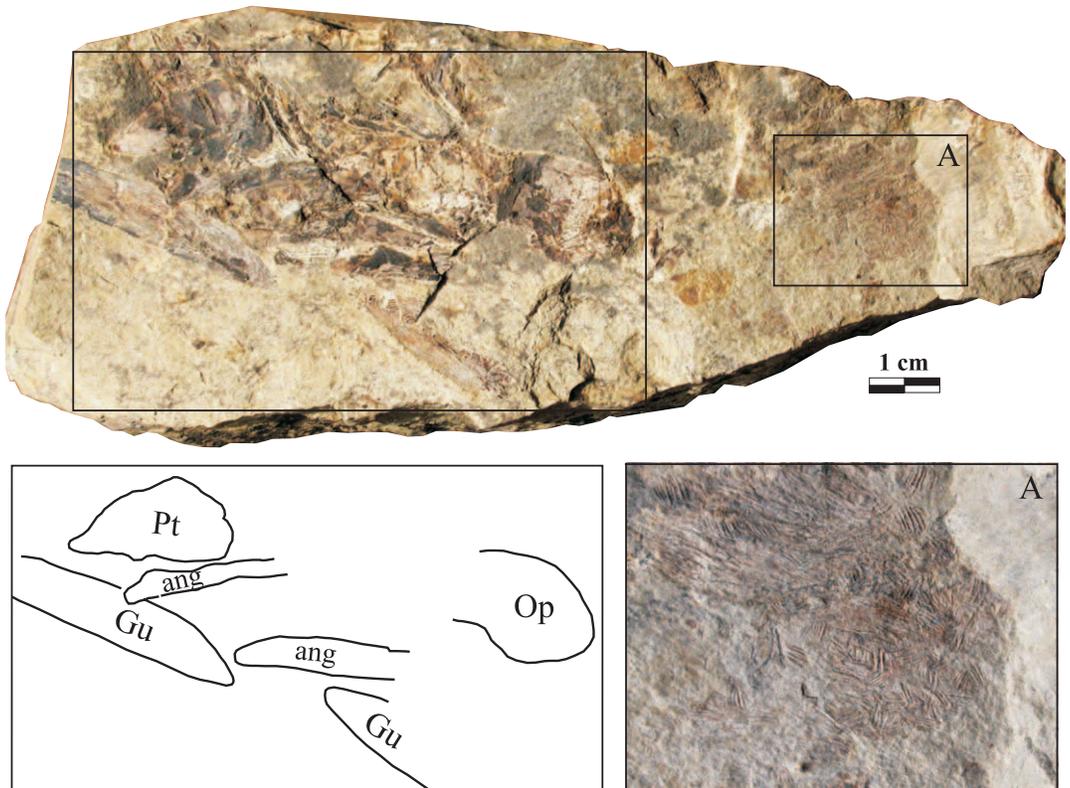


Fig. 7. *Diplocercides* sp.; MZ VIII Vp-386; Kadzielnia Quarry, Kielce; Association of carcasses of one individual. Abbreviation: ang - angular plate, Gu – gular plate, Op – operculum, Pt – entopterygoid

species based on that element only, but it is probable that specimen MZ VIII Vp-382 belongs to *Diplocercides*. Specimen MZ VIII Vp-386 (Text-fig. 7) represents an association of poorly preserved remains belonging to one individual, of which only the scales show features that are not visible on the other specimens. The scales are delicate and small, about 2-3 mm diameter. The ornament consists of numerous striae and is similar to that in tail scales figured by STENSIÖ (1937, pl. 4).

OCCURRENCE: Both specimens come from the Kadzielnia Quarry, Kielce, and are middle Famennian in age (Early *Palmatolepis rhomboidea* conodont Zone).

CONCLUSIONS

The Palaeozoic coelacanth *Diplocercides* is known from the Frasnian of Germany (STENSIÖ 1937) and Central Iran (JANVIER 1977), the Lower Carboniferous of Ireland (FOREY 1998), possibly from the Famennian of South Africa (ANDERSON & al. 1999), and from the Famennian of Poland. The occurrence of Devonian coelacanth remains in the pelagic facies of the Kadzielnia range seems rather unusual in that Devonian representatives of the actinistians lived preferentially in rather shallow waters, close to the foreshore or to the reef. It is assumed, however, that by the time of deposition of the coelacanth remains (early Famennian, Early to Middle *Palmatolepis crepida* conodont Zones), several elevated tectonic blocks were still present in the area despite the general progressive drowning of the fragmented carbonate platform. Limestone

stage	localities		Coelacanth remains		Occurrence of elevated blocks	
			Wietrzna	Kadzielnia	Dalnia	Gałęzice
FAMENNIAN	<i>P. praesulcata</i>	L	Diplocercides sp.	Diplocercides kayseri, Diplocercides sp.	■	■
		M				
	E					
	<i>P. expansa</i>	L				
		M				
	E					
	<i>P. postera</i>	L				
		E				
<i>P. trachytera</i>	L					
	E					
<i>P. marginifera</i>	Lt					
	L					
E						
<i>P. rhomboidea</i>	L					
	E					
<i>P. crepida</i>	Lt					
	L					
	M					
E						
<i>Palmatolepis triangularis</i>	L					
	M					
	E					

Fig. 8. Stratigraphical ranges of coelacanths and of submarine swells represented by elevated blocks of Dalnia and Gałęzice; E – early, M – middle, L – late, Lt – latest

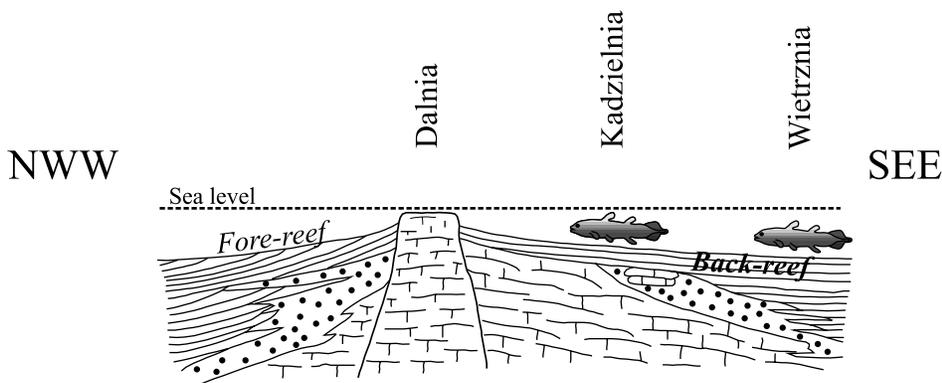


Fig. 9. Facies-bathymetric profile across the Kadzielnia chain in the Famennian (after SZULCZEWSKI 1971, text-fig. 11, modified)

neptunian dykes on the Dalia hill indicate that submarine swells existed here until the Tournaisian (SZULCZEWSKI 1973). Pelagic sedimentation probably did not begin in the Gałęzice region before the Late *P. marginifera* conodont Zone, after a long period of non-deposition or erosion (SZULCZEWSKI & *al.* 1996) (Text-fig. 8). It is possible, therefore, that the living-environment of these fishes could have been restricted to elevated areas, which were probably more numerous than are visible today (Text-fig. 9). Preservation of the coelacanth fossils in deeper-water shales could then have resulted from a relatively short-distance *post-mortem* transport of their carcasses.

As a matter of fact, the coelacanths are not the only shallow-water group of fishes which occurs in the Kadzielnia Chain: the occurrences of dipnoans in the uppermost Frasnian and lower Famennian were noted from Karczówka, Kadzielnia (GORIZDRO-KULCZYCKA 1950) and Wietrznia (WORONCOWA-MARCINOWSKA & SZREK 2004). GORIZDRO-KULCZYCKA (1950) and KULCZYCKI (1957) also mentioned the occurrence of the antiarch *Bothriolepis*, a placoderm usually found in shallow water deposits (although IVANOV & GINTER 1997, considered the specimen described by J. KULCZYCKI as a brachythoracid arthrodire).

The coelacanths constituted part of an apparently shallow-water ecosystem that thrived in the continuously deepening Late Devonian basin of the Kielce area.

It is important to undertake a systematic investigation of the Famennian vertebrate fossils, especially the osteichthyan fishes, which are currently insufficiently known in the Holy Cross Mountains.

Acknowledgements

The author is grateful to Dr. Gaël CLÉMENT (Muséum National d'Histoire Naturelle, Paris), dr. Peter FOREY Natural History Museum, London) and to Prof. Michał GINTER (Institute of Geology, Warsaw University) for comments on the early draft of the manuscript; as well as to a friend, Rafał KOWALSKI MSc (Museum of the Earth, Polish Academy of Sciences, Warsaw), for his help in providing most of the specimens presented herein.

It is a contribution to UNESCO project IGCP 491 "Middle Paleozoic Vertebrate Biogeography, Paleogeography, and Climate".

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Manuscript submitted: 15th February 2007

Revised version accepted: 30th October 2007