A large Late Devonian arthrodire (Vertebrata, Placodermi) from Poland

Piotr Szrek[a] and Olga Wilk[b]

[a] Polish Geological Institute–National Research Institute, 4 Rakowiecka Street, 00-975 Warszawa, Poland; piotr.szrek@pgi.gov.pl
[b] Faculty of Geology, University of Warsaw, 93 Żwirki i Wigury Street, 02-089 Warszawa, Poland; o.wilk@wp.pl

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Abstract. The arthrodire placoderm, *Dunkleosteus* sp., is reported from the Upper Devonian (Frasnian) of the Holy Cross Mountains, Poland. The material comprises partially preserved remains of two individuals found in the Kellwasser-like horizon of the Płucki locality. The remains are preserved as broken bone fragments redeposited from shallower environment into deep-shelf conditions. They are labelled as *Dunkleosteus* sp. and seem similar to *Dunkleosteus marsaisi* from the Famennian of Morocco. It is likely that the form from Poland represents a new species that requires further collecting and study of new specimens. The described specimens are the oldest occurrence of the genus *Dunkleosteus* in Europe, the most complete one from Poland and one of the biggest placoderms with a head about 60 cm long.

Key words: *Dunkleosteus*, Upper Devonian, Frasnian, Holy Cross Mountains, Poland.

INTRODUCTION

The genus *Dunkleosteus* (formerly *Dinichthys* in part) includes about eight species (if including *D. belgicus* (Leriche), 1931) which are found in Laurussia (USA, Canada, Belgium, Poland) and Gondwana (Morocco). The problem of the phylogenetic position of *Dunkleosteus* has been discussed by many authors (see comments in Carr & Hlavin 1995, 2010), but there is a general consensus about its affinities within Pachyosteomorphi Stensiö, 1944 and the family Dunkleosteidae Stensiö, 1944. Most of the *Dunkleosteus* material comprises more or less articulated skull roofs. This emblematic material is a rich collection from the Cleveland Shales Formation. In Europe, *Dunkleosteus* is known from the Famennian of Belgium (Leriche 1931) and Poland (Kulczycki 1957; Ivanov & Ginter 1997; Szrek 2009; Szrek & Niedźwiedzki 2015). Kulczycki (1957) described a new species of *Dunkleosteus denisoni*, based on a median dorsal plate from the middle Famennian of the Holy Cross Mountains. In 2009 Szrek also identified the same species from the so-called Kellwasser horizon (Płucki locality), uppermost Frasnian in age. All these specimens present typical features of this genus except for their small sizes. A similar situation concerns the nuchal plate illustrated by Ivanov & Ginter (1997, fig. 4B) from the Famennian of the Ostrówka quarry, which (although undescribed) represents a typical *Dunkleosteus*, but below most of Cleveland *Dunkleosteus* size. In the opinion of Ivanov & Ginter (1997) it resembles *D. marsaisi* Lehman, 1954 from the early Famennian of Morocco (Lehman 1956).

Although tens of placoderm fossil remains were collected in Płucki during long-term excavation works between 1996 and 2006 (see Szrek 2008, 2009; Szrek & Niedźwiedzki 2015; Dworczak & Szrek 2016), only few specimens have been described formally. The first data about placoderms from Płucki were presented by Ivanov & Ginter (1997) who initially described a partly preserved skull-roof of an eastmanosteid arthrodire. Later, Szrek (2007a, 2007b, 2008) and Szrek & Ginter (2008) mentioned the Płucki placoderm assemblage but the first detailed description was published by Dworczak & Szrek (2016) who described remains of *Aspidichthys ingens* Koenen, 1883. Most of the material is described in the unpublished PhD thesis of Szrek (2009).

The aim of the present paper is therefore to describe a new material of *Dunkleosteus*, initially identified by Szrek (2009), but not formally described. The material includes the largest representatives of the Polish placoderms and comprises head- and trunk-shield elements.

GEOLOGICAL SETTING

The source locality of the reported material is located in the Płucki village near the town of Łagów in the central part of the Holy Cross Mountains (central Poland, Fig. 1). This locality represents important strata of the

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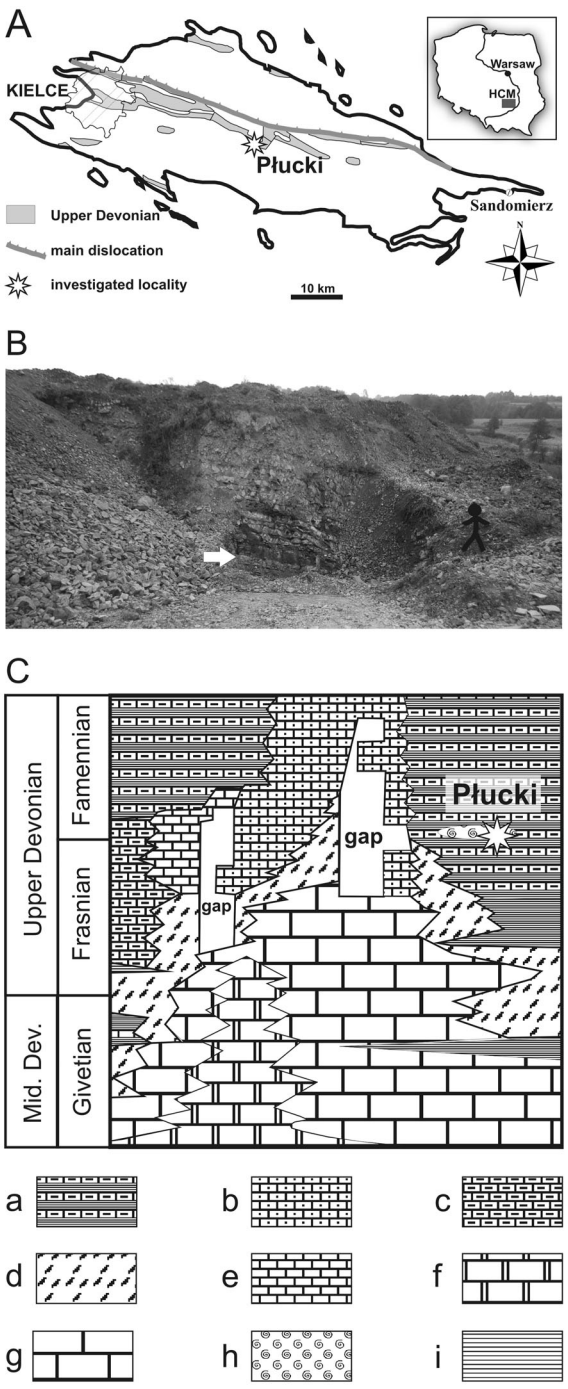

Fig. 1. The investigated outcrop in Płucki. **A**, location map in the Holy Cross Mountains (HCM), Central Poland (modified from Kowalczewski 1971). **B**, general picture of the outcrop; the place of the fossil-bearing horizon is marked with an arrow. **C**, diagrammatic cross section through the Holy Cross Mountains from the Givetian to the top of the Upper Devonian (modified after Szulczewski 1995) with the probable position of the investigated localities (a, marly limestones and shales; b, condensed cephalopod and crinoidal limestones; c, marly limestones; d, calcirudites; e, bedded limestones; f, dolomites; g, massive and bedded limestone; h, cephalopod limestones; i, clayey and marly shales).

Frasnian–Famennian boundary. The first report about the Płucki locality was given by Sobolev (1912) and Czarnocki (in the 1920s, general geology field notes – unpublished until 1989), followed by Makowski (1963, 1971) and Dzik (1985) who described a rich goniatite fauna within black bituminous limestone. The first published details about the section exposed in the Płucki site were due to Szulczewski (1989) who used for the first time the term 'Upper Kellwasser Limestone', labelling a black bituminous limestone horizon. Then several papers on the stratigraphy, geochemistry and palaeontology of the site were published by Bond et al. (2004), Dworczak & Szrek (2016), Dzik (2002), Filipiak (2002), Ginter (1995, 2002), House (2002), Ivanov & Ginter (1997), Racki et al. (2002), Szrek (2007a, 2007b, 2008, 2009), Szrek & Ginter (2008), Woroncowa-Marcinowska (2006) and Rakociński et al. (2016). This locality was also a source of material for few scientific projects and MSc and PhD theses by Janiszewska (2008), Szrek (2009) and Dworczak (2016).

The section studied in the Płucki outcrop is about 5 m thick and resembles the Kellwasser-like horizon. The entirely Frasnian lower part (up to 30 cm) is characterized by marls at the bottom with limestone above. The limestone middle part (up to 10 cm) is rich in cephalopods and arthrodire placoderms. According to the detailed analysis of Janiszewska et al. (2007), the Frasnian–Famennian boundary is putatively situated within this part of the horizon. The uppermost part entirely belongs to the Famennian and is characterized by abundant invertebrate and fish material. Part of the internal structure of the Kellwasser-like horizon is characterized by the occurrence of a breccia-like structure (unpublished data by P. Szrek and S. Salwa). It is composed of few lithological components: big fragments of solid black dolomitic limestone of fossiliferous and non-fossiliferous types occur in the form of clasts and are surrounded by less-solid dark brown limestone. Bones within the horizon reflect signs of pre-fossilization damage of potential mechanic origin. It is expressed by the occurrence of broken bones surrounded by the sediment. This points to a damage before final burial.

Fossils are much less numerous or absent above the Kellwasser-like horizon. They comprise only pelagic invertebrates.

MATERIAL AND METHODS

The material analysed consists of seven described specimens representing isolated parts of disarticulated head and trunk shields. The fragmentary condition of the material precludes authors to perform a cladistic analysis beyond the proposed systematic attribution.

Two accumulations of big skeletons have been ascertained within the Frasnian part of the Kellwasser-like horizon. These skeletons are disarticulated, however, it seems that they particularly represent single individuals.

The material collected comprises therefore putative associations of two individuals. Association 1 consists of the posterior part of a skull roof including the nuchal plate and partly preserved paranuchal (mostly left one) and central plates (Muz. PGI-NRI 1809.II.18, Fig. 2A–C), both partially preserved anterior dorsolateral plates (Muz. PGI-NRI 1809.II.20,21; Fig. 3A, B and the right suborbital plate (Muz. PGI-NRI 1809.II.22; Fig. 3C, D). Association 2 comprises the posterior part of a skull roof including the nuchal plate and partly preserved paranuchal and central plates (MWG UW ZI/43/0053, Fig. 4A, B), a fragment of a left central plate associated with part of the pineal plate (Muz. PGI-NRI 1809.II.23; Fig. 4C) and a median dorsal plate preserved in most of its original shape (Muz. PGI-NRI 1809.II.19, Fig. 5).

All specimens are preserved 3-dimensionally. Features of their preservation point to a pre-fossilization damage shown by the broken margins covered by the sediment. According to the recent interpretation of the origin of the Płucki section (unpublished data by P. Szrek and S. Salwa, see also Dworczak & Szrek 2016), it is likely that the bones were redeposited to their place of final burial from the shallower environment, during a slump event.

The material is housed in the Geological Museum of the Polish Geological Institute–National Research Institute, Warsaw (abbreviated Muz. PGI-NRI) and at the Faculty of Geology, University of Warsaw, Warsaw (abbreviated MWG UW).

SYSTEMATIC PART

Class PLACODERMI M'Coy, 1848
Order ARTHRODIRA Woodward, 1891
Family DUNKLEOSTEIDAE Stensiö, 1963
Genus *Dunkleosteus* Lehman, 1956

Dunkleosteus sp.
Figures 2–5

Age. Upper Devonian, uppermost Frasnian, *Palmatolepis linguiformis* conodont Zone.

Description. Specimen Muz. PGI-NRI 1809.II.18 (Figs 2A, B, 6A) represents the posterior part of the head and comprises the nuchal plate, part of the left paranuchal and very partially preserved central plates. The external surface is strongly abraded and natural boundaries are difficult to distinguish. The posterior margin of the nuchal plate is slightly embayed and has a single posteromedian process (Figs 2B, 6A). The anterior margin of this plate that contacts with the central plates bears a prominent wide V-shaped projection between both central plates. The side margins of the nuchal plate are more or less straight. Its posterolateral wings are well visible. Its visceral side is also partially abraded, especially in the anterior portion and there is no visible contact of the nuchal plate with the centrals. The levator pits are ellipsoidal in shape and about 1.4 cm wide, however, their shape may have been modified by erosion. They are separated by the median septum which is about 1 cm wide. They are bounded anteriorly by the huge transverse occipital thickening (3.7 cm at the thickest point) and posteriorly by a poorly developed and narrow transverse ridge of about 0.5 cm wide. Part of the left paranuchal is preserved and provides the morphology of the lateral articular fossa and partially, the para-articular process. The lateral articular fossa is ellipsoidal in shape and is 7.2 cm wide and about 2 cm deep. The para-articular process is broken at the base. The transverse occipital thickening of the nuchal plate is continuing that of the paranuchal plates which are preserved on the both sides of the specimen. Internal and external openings of the endolymphatic duct are also preserved (Fig. 6B). The internal opening is located about 1 cm ahead towards levator pits at the base of the occipital thickening (Fig. 2B). The external opening is visible about 1.5 cm from the posterior margin of the paranuchal plate (Fig. 4B). On its outer surface the paranuchal plate carries the sensory line grooves for the main lateral line and posterior pitline. Their connection is not preserved but it seems that they meet at about 80°. Parts of two poorly preserved anterior dorsolateral plates (Muz. PGI-NRI 1809.II.20 – right, Muz. PGI-NRI 1809.II.21 left; Fig. 3A, B) and the right suborbital plate (Muz. PGI-NRI 1809.II.22) have been found in association with specimen Muz. PGI-NRI 1809.II.18 (Fig. 2A–C). The suborbital plate comprises the suborbital lamina preserved only in its anteriormost part and the blade which seems to be preserved completely but is strongly eroded. The blade is about 18 cm long and its maximum width reaches 4 cm. The lamina for the posterior supragnathal is well visible, especially on the cross section (Fig. 3D, D1). Anterior dorsolateral plates have no natural margins and the only feature well recognizable is a broken glenoid condyle.

Specimen MWG UW ZI/43/0053 (Fig. 4A, B) represents a mostly preserved nuchal plate with very partially preserved paranuchal and right central plates. Both the visceral and outer surfaces are well visible. This specimen is 27 cm wide and 18 cm long. The nuchal plate outline is trapezoidal with a transverse anterior margin, however, a poorly visible V-shaped incision is observed between centrals. On the right side of the outer

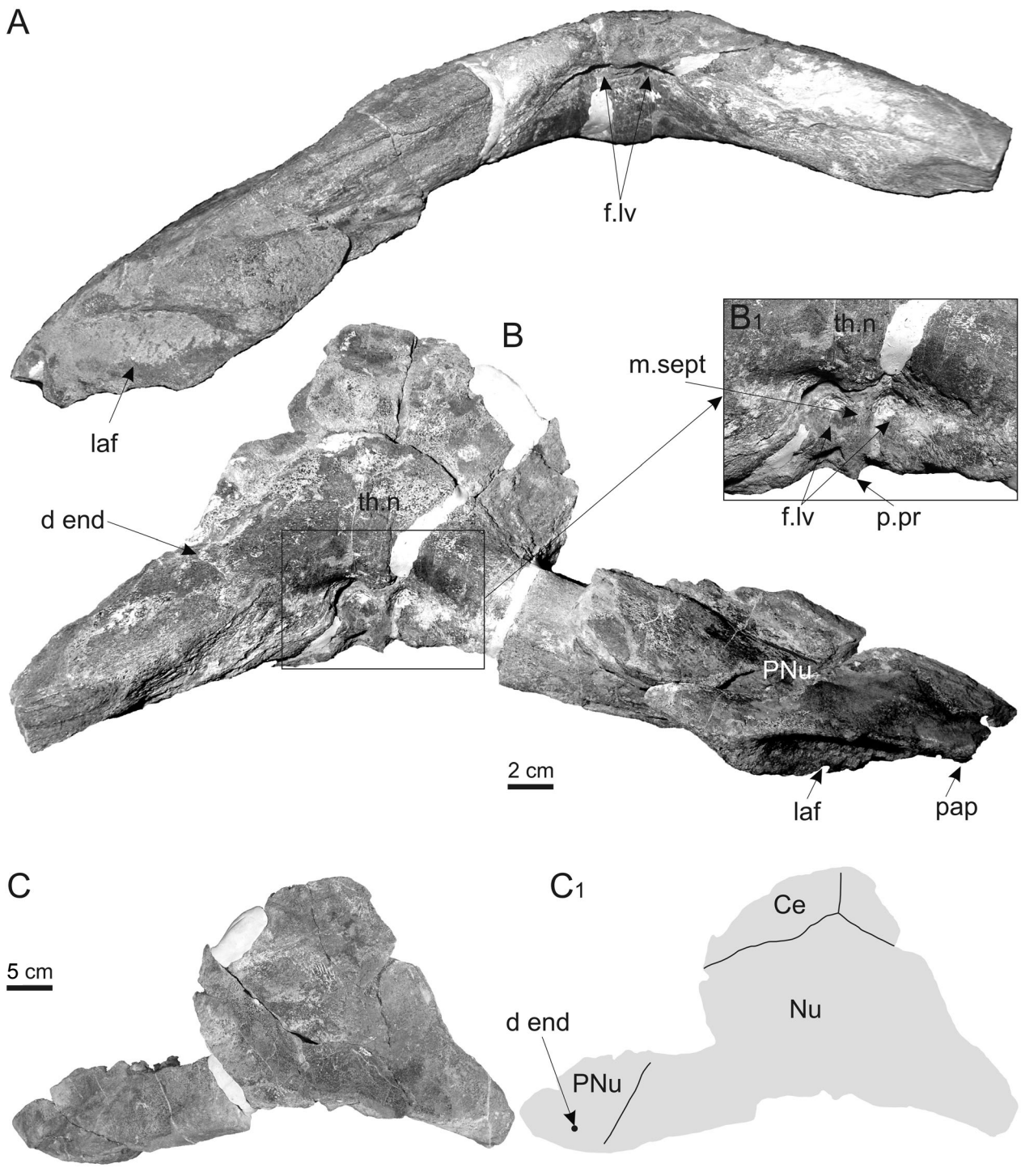

Fig. 2. Fragments of the head shield of *Dunkleosteus* sp. **A**, specimen Muz. PGI-NRI 1809.II.18, back view. **B**, specimen Muz. PGI-NRI 1809.II.18, visceral view. **B1**, magnified fragment of fig. B. **C**, specimen Muz. PGI-NRI 1809.II.18, external view. **C1**, sketch of the external view of the specimen on C. Abbreviations for Figs 2, 4 and 6: Ce, central plate; d end, opening of the endolymphatic duct; dp. m. cu., cucullaris depression; f.lv, levator pits; laf, lateral articular fossa; m.sept, median septum; Nu, nuchal plate; PNu, paranuchal plate; pap, para-articular process; p.pr, posterior process of the nuchal plate; PrO f., contact face for the preorbital plate; ppt, pineal pit; th.n, nuchal thickening; th.pre, pre-endolymphatic thickening.

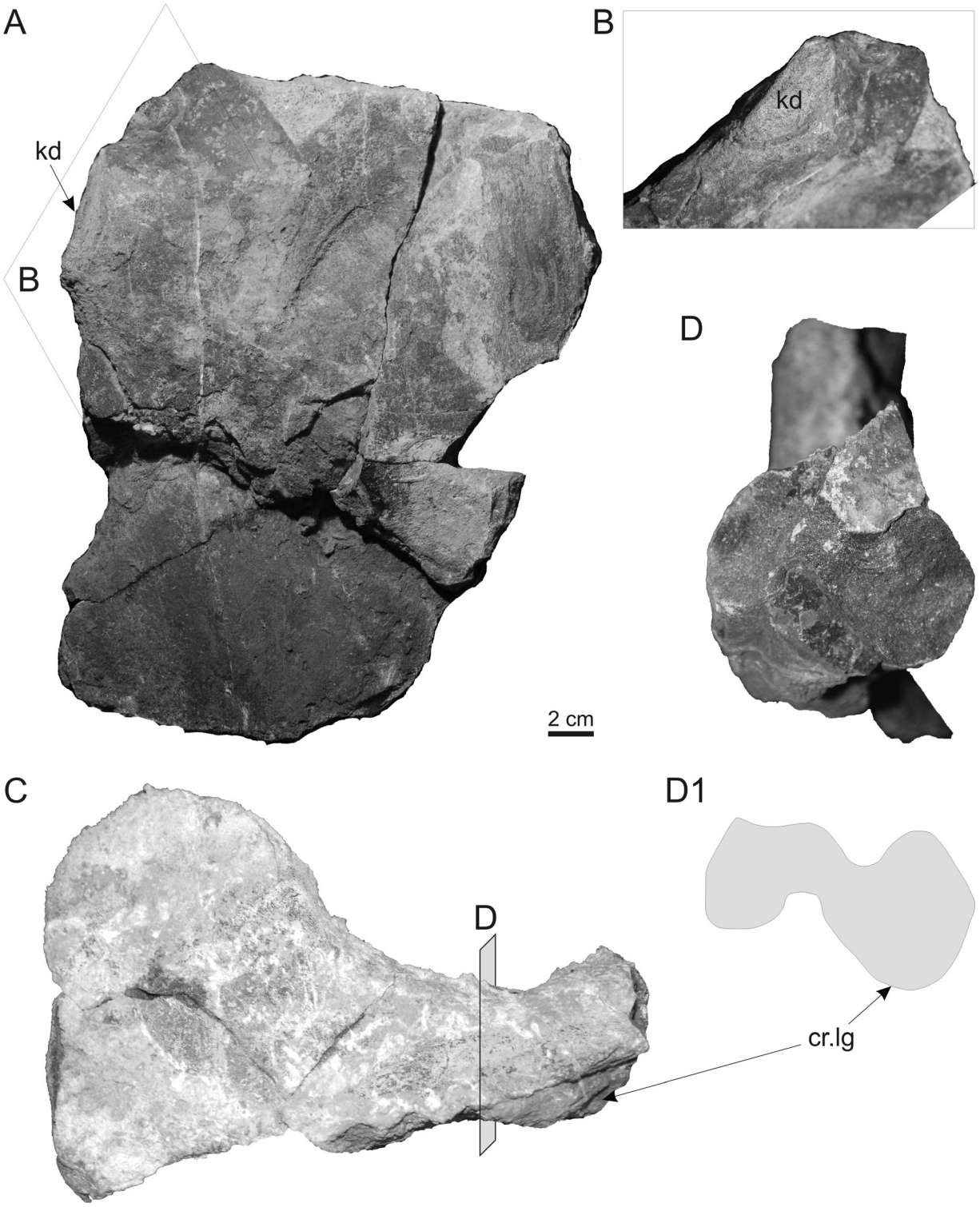

Fig. 3. A, specimen Muz. PGI-NRI 1809.II.20 right anterior dorsolateral plate (ADL) in visceral view. **B**, magnified area marked on A with a broken glenoid condyle (kd) area. **C**, specimen Muz. PGI-NRI 1809.II.22, right suborbital plate in external view. **D**, cross section of the part of the lower part of the suborbital plate (marked on C). **D1**, outline of the cross section illustrated on D with the linguiform process (cr.lg) marked.

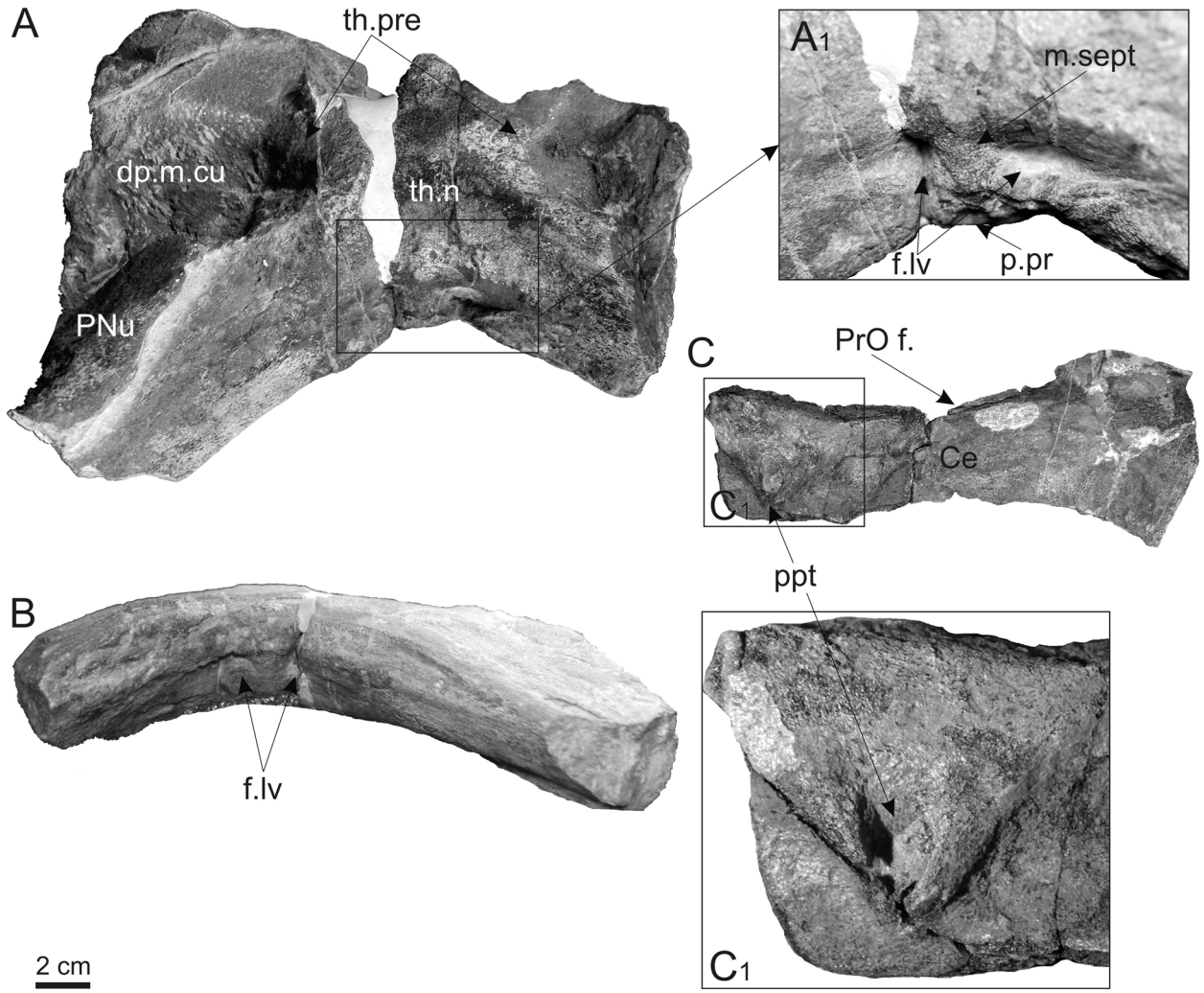

Fig. 4. A, specimen MWG UW ZI/43/0053, visceral view. **A1**, magnified fragment of fig. A. **B**, specimen MWG UW ZI/43/0053, back view. **C**, specimen Muz. PGI-NRI 1809.II.23, fragment of the pineal and left central plates. **C1**, magnified area of the pineal plate marked on C. See Fig. 2 for the explanation of abbreviations.

surface the boundary of the nuchal plate and paranuchal plates is recognizable. Its course is straight and starts from the posterior margin of the plate (not preserved) and runs towards the front with a gentle curve directed to the symmetry axis. This part is about 15.5 cm long and then turns to the left at about 90–95°. This part is visible at a distance of only 4 cm and has transverse, gently undulating shape directed towards ahead. Based on proportions, it seems that the anterior margin of the nuchal plate might be about 18 cm long. Features of the paranuchal and very partially preserved central plates are very limited for analysis because neither sensory canals nor openings are visible. Moreover, the boundary between the central and paranuchal plates is uncertain. The entire outer surface is smooth, without tubercles. The internal surface possesses a well-developed transverse occipital thickening (Fig. 4A). It is correlated with the thickening of the paranuchal plates which is preserved on the right side of the specimen. Levator pits have ellipsoidal shape with the longer axis about 1.3 cm parallel to the posterior margin of the plate. They are bounded anteriorly by the transverse occipital thickening and posteriorly by a poorly developed narrow transverse ridge about 0.6 cm wide. The levator pits are separated by a prominent median septum about 1.7 cm wide. The transverse occipital thickening is continuing on the paranuchal plate. Anteriorly to the occipital thickening there occurs the cucullaris depression which is about 0.5 cm thick in its thinnest point in the middle of the depression. It is bounded anteriorly by a not very prominent pre-endolymphatic thickening. The paranuchal margin is visible on the visceral side and shows that the

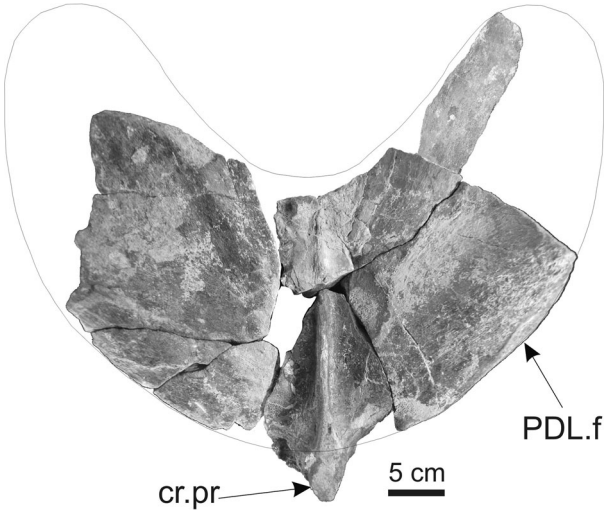

Fig. 5. Specimen Muz. PGI-NRI 1809.II.19, median dorsal plate in visceral view. Abbreviations: cr.pr, carinal process; PDL.f, contact face for the posterior dorsolateral plate.

nuchal plate has large overlap areas on the visceral surface for the central and paranuchal plates. Specimen Muz. PGI-NRI 1809.II.23 (Fig. 4C) is a partially preserved fragment of the anterior part of the left central plate associated with part of the pineal plate. The anterior margin shows elongated contact faces for the posterior margin of the preorbital plate. This margin is transverse and gently curved backwards. On the visceral side the deep depression of the pineal pit is bordered posteriorly and laterally by a ridge which is opened anteriorly (Fig. 4C1). No natural margins could be recognized due to the high degree of abrasion of both surfaces of the specimen.

A median dorsal plate has been found in association with the nuchal described above. Specimen Muz. PGI-NRI 1809.II.19 (Fig. 5) is partially preserved but shows the almost complete morphology of the plate. The plate is broken into several pieces. The posterior part and the uncomplete anterior part show a natural margin. The plate is relatively big: its preserved part is about 50 cm long measured from the natural anterior margin to the broken carinal process and a maximum of about 45 cm wide. The external surface lacks tubercles. The hind margin is rounded. The anterior margin forms a deep and rounded embayment of the posterior part of the nuchal gap. This plate is strongly arched transversely: the anterior part is gently curved, but the posterior lateral sides meet together at an angle of about 80° and form a crest. The keel on the visceral side is well visible along the entire plate, starting from the most anterior part where it forms a delicate and thin septum (about 0.2 mm). The posterior part becomes thicker and finally forms

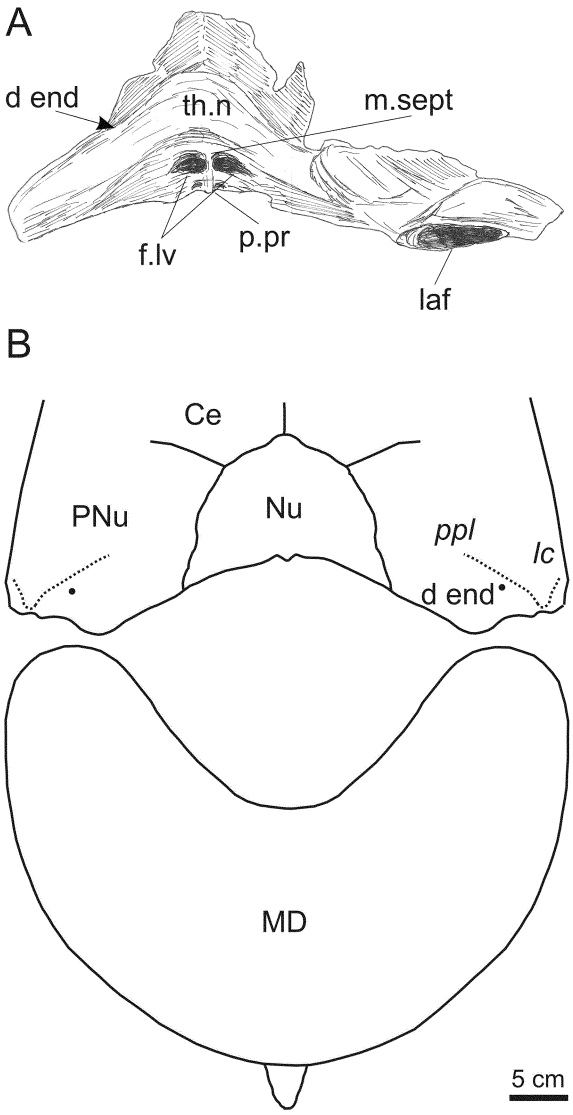

Fig. 6. A, sketch of specimen Muz. PGI-NRI 1809.II.18 in visceral view. **B**, restoration of the part of the head shield and the median dorsal plate. Abbreviations: *lc*, main lateral-line canal; MD, median dorsal plate; *ppl*, posterior pit line; for the rest see Fig. 2.

a carinal process which is broken almost at the base. There are elongated contact faces on the posterolateral margins of the plate for the posterior dorsolateral plates.

Discussion. The described specimens, especially the nuchal plates, clearly represent the genus *Dunkleosteus* and differ from other big arthrodires (after Lehman 1956, Denison 1978 and Dennis-Bryan 1987) in the emarginated posterior border of the skull roof, paranuchal plates extending back beyond the nuchal plate and showing a para-articular process, lack of dermal ornament, short, broad and triangular nuchal plate. The ventral

surface of the head shield has a massive nuchal thickening and lateral consolidated parts. Levator pits are situated posteroventrally and separated by a well-developed median septum. Moreover, the median dorsal plate has a massive keel and carinal process. The anterolateral plates have large lateral laminae. Those features, including also the big size, distinguish the described specimens from other arthrodires, especially from *Eastmanosteus* (see discussion in Dennis-Bryan 1987 and Carr & Hlavin 2010).

Specimens MWG UW ZI/43/0053 (Fig. 4A, B), Muz. PGI-NRI 1809.II.19 (Fig. 2A, B) and Muz. PGI-NRI 1809.II.23 (Fig. 4C) putatively represent one individual and similarly another association of specimens Muz. PGI-NRI 1809.II.18 (Fig. 2A, B), Muz. PGI-NRI 1809.II. 20, 21 (Fig. 3A, B) and 22 (Fig. 3C, D). There is of course a possibility that all fragments represent different fishes and species as well. It was one of the reasons why we have decided to leave the identification rather tentative.

The nuchal plate in both cases described above has a rectangular anterior margin with a V-shaped incision between centrals (see Muz. PGI-NRI 1809.II.18; Fig. 2C1, 6B) and moreover a deep overlap area for the central and paranuchal plates. These are characteristic features of *Dunkleosteus* (compare Heintz 1931, 1932, text-fig. 12; pl. 1) which brings the Polish specimens closer to *Dunkleosteus marsaisi* (Lehman 1956, pl. 6; or Moroccan *D. terreli* if is synonymized with *D. marsaisi* (Lehman, 1954) from Morocco (Rücklin 2002)) and *Dunkleosteus* sp. illustrated by Ivanov & Ginter (1997, fig. 4B). The nuchal plate outline fits well with *Dunkleosteus marsaisi* (Lehman 1956, fig. 8) and *D. intermedius* (*terreli*) (Heintz 1932, text-fig. 12) but is narrower. It resembles the nuchal plate of *D. amblyodoratus* Carr & Hlavin, 2010 (fig. 6A–C) also in size, however, Polish specimens have a more prominent anterior part. Also, the occipital thickening is roughly typically developed and resembles many specimens referred to *Dunkleosteus*. Both the described nuchal plates are characterized by a similar development of the levator pits areas which show the same thin transverse ridge that is bounding pits posteriorly. In specimen MWG UW ZI/43/0053 (Fig. 4A) this ridge is almost incorporated into the posterior margin of the plate, whereas it is more prominent in specimen Muz. PGI-NRI 1809.II.18 (Fig. 2A, B). This difference may be ontogenetic because specimen MWG UW ZI/43/0053 (Fig. 4A) is larger and therefore may represent an older stage than PGI-NRI 1809.II.18 (Fig. 2A, B). Anyway, this feature (pits bounded by the ridge are small posteriorly or almost absent) is unusual for *Dunkleosteus* (e.g. Carr & Hlavin 2010, fig. 6A, B) and occurs not very often. A similar case was illustrated by Lehman (1956, pl. 16F), who identified his fragmentary specimen as Dinichthyidae *sensu lato*. The shape and morphology of levator pits on specimen Muz. PGI-NRI 1809.II.18 (Fig. 2A1), which are more rounded than ellipsoidal and are bounded posteriorly by a very thin transverse ridge, are similar to features present also in the specimen illustrated by Lehman (1956, pl. 16F). A comparable feature occurs in some undescribed specimens stored in the Famennian part of the collection, in the Cleveland Natural History Museum. This may be a diagnostic character for a new species that must be carefully studied in the future based on additional material.

The morphology of the suborbital plate cannot be recognized in details, especially due to the suborbital lamina. The postorbital region is partially preserved but the cross section illustrates well the prominent linguiform process that is common within the genus (e.g. Dean 1908, fig. 60; Heintz 1932, text-figs 21, 22).

The median dorsal plate resembles the *Dunkleosteus* pattern in its outline (e.g. Dean 1908, fig. 61) but is different from most of the dunkleosteid median dorsal plates (see Heintz 1932, text-fig. 44; Lehman 1956, pl. 14). However, anterolateral margins are not recognized; they must have had deep embayment in the anterior part comparable to that of *D. marsaisi* (Lehman 1956, pl. 14B). The development of the keel on the specimen analysed is quite typical for the genus. It is present along almost the entire plate and gradually becomes crude at the posterior margin with the carinal process, resembling the specimens of *Dunkleosteus* illustrated by Heintz (1932, text-fig. 44). The comparison with other material from the Holy Cross Mountains indicates different affinities. The specimens of *Dunkleosteus denisoni* described by Kulczycki (1957: 313, text-fig. 10, pl. VI, fig. 4, fig. VII) represent a much smaller taxon which possesses a huge keel and carinal process. Though, even if the keel and process are broken, it is clear that these were not very prominent in the specimen described herein (comp. Kulczycki 1957, pl. VII and Fig. 5). Moreover, specimens described by Kulczycki (1957) are middle Famennian in age.

Other features like the morphology of the transverse occipital thickening, cucullaris depression, the morphology of the internal side of the pineal opening and the position of the external and internal opening for the endolymphatic duct fit to the general morphology of the genus *Dunkleosteus* illustrated by Leriche (1931), Heintz (1932, text-figs 12, 13, pls 1, 2) and Stensiö (1963, fig. 112A, B).

The reconstructed width of the skull is about 50 cm. Based on proportions of the best-preserved specimens from the Cleveland collection it is likely that the form described from the Holy Cross Mountains reached more than 60 cm in skull length and is a bit larger than *D. marsaisi* (skull length about 50 cm).

CONCLUSIONS

The described specimens represent the oldest occurrence of the genus *Dunkleosteus* in Europe, being uppermost Frasnian in age. Moreover, it is the first *Dunkleosteus* from Poland described with certainty based on skull remains. The material is preserved in associations with two individuals which probably represent the same taxon at different ontogenetic stages.

According to essential features, these specimens are closest to *Dunkleosteus marsaisi* (Lehman 1956) by the external shape and internal morphology of the nuchal plate, internal morphology of the pineal plate and similar sizes. The Polish specimen differs from the Moroccan one in the development of the levator pits area, which may be a specific character for the possible distinction of a separate species of *Dunkleosteus*.

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Suur Hilis-Devoni artrodiir (Vertebrata, Placodermi) Poolast

Piotr Szrek ja Olga Wilk

On kirjeldatud Placodermi klassi kuuluvat artrodiiri *Dunkleosteus* sp., kelle jäänukid leiti Ülem-Devoni (Frasnesi) nn Kellwasseri taseme kivimitest Płucki paljandist Świętokrzyskie mägedest Poolast. Kahe isendi osaliselt säilinud jäänukid on ilmselt ümber setitatud madalaveelisemast faatsiesest süvašelfi alale. Leitud fragmendid on siin nimetatud *Dunkleosteus* sp., kuid nad on sarnased *Dunkleosteus marsaisi*'le Maroko Famenne'ist. See viitab, et Poola vorm võib olla uus liik, kuid selle tõestamine vajab lisamaterjali leidmist ja uurimist. Kirjeldatud eksemplarid on *Dunkleosteus*'e perekonna vanimad esindajad Euroopas, kõige täielikumad Poolas, kuuludes suurimate plakodermide hulka, kelle pea on 60 cm pikk.