



## **The First Lower Jaw of a Ctenacanthid Shark from the Late Devonian (Famennian) of Belgium**

Authors: Wilk, Olga, Olive, Sebastien, Pradel, Alan, Den Blaauwen, Jan L., and Szrek, Piotr

Source: Journal of Vertebrate Paleontology, 41(3)

Published By: The Society of Vertebrate Paleontology

URL: <https://doi.org/10.1080/02724634.2021.1960537>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.






Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## THE FIRST LOWER JAW OF A CTENACANTHID SHARK FROM THE LATE DEVONIAN (FAMENNIAN) OF BELGIUM

OLGA WILK, <sup>1,2\*</sup> SEBASTIEN OLIVE, <sup>3</sup> ALAN PRADEL, <sup>4</sup> JAN L. DEN BLAAUWEN, <sup>5</sup> and PIOTR SZREK <sup>1</sup>;  
<sup>1</sup>Polish Geological Institute-National Research Institute, 4 Rakowiecka Street, 00-975 Warsaw, Poland owl@pgi.gov.pl; <sup>2</sup>Faculty of Geology, University of Warsaw, 93 Żwirki and Wigury Street, 02-089 Warsaw, Poland; <sup>3</sup>Earth & History of Life Directorate, Royal Belgian Institute of Natural Sciences, Rue Vautier 29, 1000 Brussels, Belgium; <sup>4</sup>Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Unité Mixte de Recherche 7207 du Centre National de la Recherche Scientifique, 47 Rue Cuvier 75231 Paris Cedex 05, France; <sup>5</sup>University of Amsterdam, Science Park 904, 1098XH, Amsterdam, the Netherlands

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

Citation for this article: Wilk, O., S. Olive, A. Pradel, J. L. den Blaauwen, and P. Szrek. 2021. The first lower jaw of a ctenacanthid shark from the Late Devonian (Famennian) of Belgium. *Journal of Vertebrate Paleontology*. DOI: [10.1080/02724634.2021.1960537](https://doi.org/10.1080/02724634.2021.1960537).

The internal skeleton of “conventionally defined” Chondrichthyes (i.e., chondrichthyans excluding acanthodians; Zhu et al., 2013) is built up of calcified cartilage, which is characterized by a very low fossilization potential and is thus very rarely represented in the fossil record. On the other hand, other isolated elements of the body, such as teeth, spines and dermal denticles, that are built up of dentine, constitute the majority of the chondrichthyan remains found in the sediments. Elements of fossilized cartilage and articulated skeletons are very rare in the Paleozoic era. Therefore, even the smallest element of endoskeleton is interesting and important to enrich our knowledge about Paleozoic sharks.

Most of the Paleozoic chondrichthyan remains are known from Carboniferous deposits but shark-like scales are found as early as the Ordovician and Silurian (Sansom et al., 1996; Young, 1997; Johanson et al., 2008; Sansom et al., 2012; Andreev et al., 2016a, 2016b). The oldest articulated shark remains comprising tooth families, braincase, fin spines, and squamation belong to *Doliodus latispinosus* from the Lower Devonian (early Emsian, ca. 409 Ma) of Canada (Miller et al., 2003, Burrow et al., 2017). Other Early Devonian sharks represented by isolated braincases with parts of the visceral skeleton are *Pucapampella* and *Gydoselache* from Bolivia and South Africa (Janvier and Suárez-Riglos, 1986; Maisey, 2001; Maisey and Anderson, 2001; Pradel et al., 2009; Janvier and Racheboeuf, 2018; Maisey et al., 2019). Younger endoskeleton remains, *Gladbachus adentatus* from the Middle Devonian (Givetian ca. 385 Ma), were found in Germany (Coates et al., 2018). Late Devonian extinctions which affected mainly placoderms and stem-chondrichthyan acanthodians allowed for rapid evolution and development of “conventionally defined”

chondrichthyans (Benton, 2005). Thus, shark remains from the Late Devonian and Carboniferous occur much more commonly and have been studied by many authors to date (e.g., Lund, 1974; Zangerl, 1981; Williams, 1985; Maisey, 1989; Yazdi and Turner, 2000; Pradel et al., 2014; Long et al., 2015; Frey et al., 2020). One of these localities is Cleveland (Ohio) where many almost complete Late Devonian sharks have been found, i.e., *Cladoselache*, *Monocladodus*, *Stethacanthus*, *Tamiobatis*, and *Ctenacanthus* (Newberry, 1889; Clappole, 1893; Harris, 1938; Williams, 1998; Tomita, 2015). One specimen from the Upper Devonian (early Frasnian) Gogo Formation, Western Australia, is assigned to *Gogoselachus lynnbeazleyae*, and it includes three-dimensionally preserved Meckel's cartilages, nasal, ceratohyal, basibranchial and possible epibranchial cartilages, plus left and right scapulocoracoids, as well as teeth and scales (Long et al., 2015).

Late Devonian fishes from Belgium have been studied by many authors (e.g., Gross, 1965; Lelièvre, 1982; Blicek and Lelièvre, 1995; Cloutier and Candilier, 1995; Derycke et al., 1995; Clément, 2002; Clément et al., 2004; Janvier and Clément, 2005; Derycke and Clément, 2013; Derycke et al., 2014; Olive, 2015; Olive et al., 2015a, 2015b, 2020; Ginter et al., 2017). Our knowledge of the Famennian vertebrates from Belgium is mainly restricted to the late Famennian (fluvio-lagunal Evieux Formation) whereas the more distal Montfort Formation has received much less attention regarding its vertebrate content. Olive (2015) and Olive et al. (2015a) discussed placoderm material with indistinct Montfort/Evieux formations assignments. However, regarding cartilaginous fishes from the Late Devonian of Belgium our knowledge is based mainly on teeth and scales. Derycke-Khatir (1994) and Derycke et al. (1995) mentioned dentine elements from the Famennian which belong to *Ctenacanthus* sp., *Lissodus* sp. cf. *L. zideki*, *Phoebodus* spp., *Protacrodus* sp. cf. *P. vetustus* and *Protacrodus* spp. Later, Derycke et al. (2014) described several additional genera (*Bobbodus*, *Campodus*, *Orodus*, *Stethacanthus*) from the Ardenne Massif. Ginter et al. (2017) described a classic Late Frasnian chondrichthyan assemblage (scales and teeth) from southern Belgium where three different genera have been reported, i.e., *Phoebodus*, *Cladodoides* and *Protacrodus*.

Herein, we describe the first occurrence – other than teeth and scales – of a possible ctenacanthid shark (right Meckel's

\*Corresponding author.

© 2021, Olga Wilk, Sebastien Olive, Alan Pradel, Jan L. Den Blaauwen, Piotr Szrek.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

cartilage) from the Upper Devonian (Famennian) of the Liège Province, Belgium. It is the first fossilized element of the internal skeleton found in the Upper Devonian of continental Europe. Despite the lack of characteristic features which could allow an accurate specific assignment, it is likely that the examined specimen belongs to one of the species that have already been described from Belgium.

## GEOLOGICAL SETTING

In Belgium, Famennian rocks crop out extensively across the Dinant Synclinorium (allochthonous), which is a Variscan structural element of the Namur-Dinant Basin. The Famennian shows a regressive trend from open marine shales of the Famenne Group (lower Famennian) to fluvio-lagoonal siltstones, sandstones and dolomites of the Upper Famennian Evieux Formation (Thorez and Dreesen, 1986). The litho- and biostratigraphy of the stage are well known, thanks to the seminal works of Thorez and colleagues (Thorez et al., 1977, 2006; Thorez and Dreesen, 1986, 2002), which were mainly dedicated to the Condroz area (eastern Dinant Synclinorium).

The lower jaw studied in this paper comes from the “Thomas quarry,” left bank of the Ourthe River near Poulseur and Montfort, Province of Liège, Belgium, within the Dinant Synclinorium (Fig. 1). The mandible was found in an isolated block of hard sandstone, difficult to place in the stratigraphic sequence. The stratigraphic interval of the quarry is between the Montfort Formation and the base of the Evieux Formation (Thorez and Dreesen, 2002), thus a late Famennian age can be attributed with certainty to the material, but it is impossible to precisely assign our isolated material to one of the formations. The Montfort Formation is dominantly composed of light to dark gray, thickly bedded arkosic sandstone, with some shaly intercalations. It records several interdigitated environments (defined as members; Thorez et al., 1977, 1988): the sandy barrier, the fore-barrier sandy flat and the back-barrier lagoon with evaporite sabkha-type dolomite. The Evieux Fm is heterolithic and defined by numerous occurrences of red beds and paleosols (Royseux Mb) and alluvial channel complex (Crupet Mb), both including primary dolomite horizons.

## MATERIAL AND METHODS

The examined specimen, which consists of an isolated right Meckel’s cartilage (lower jaw) of a putative ctenacanthid shark without other co-occurring remains or teeth, was collected by a workman (Christian Mancini) of the “Thomas quarry” and given to the “Ardennen research group.” This group comprised scientists interested in the geology and paleontology of the Famennian of the Ardennes, Belgium, who collected material in this area between 1980 and 2001. All members were from the University of Amsterdam and included Dr. P. H. de Buissonjé, O. J. Simon, F. Storbeck, F. A. Nobel and one of the authors of the present paper, J. L. den Blaauwen, who is still working in this university. Much later, in 2016–2017, the material of these expeditions was given to the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium. The lower jaw is housed in the paleontological collections of this institution under the number IRSNB P 9956.

The Meckel’s cartilage was mechanically prepared by J. L. den Blaauwen with medium-sized and tiny diamond drills. Cracks were filled with epoxy resin. Recently, the specimen was virtually observed by conventional X-ray tomography at the RBINS to investigate unprepared regions and internal features, using a RX EasyTom instrument (RX Solutions, Chavanod, France; [www.rxsolutions.fr](http://www.rxsolutions.fr)) with a copper filter. Images were generated at a voltage of 150 kV and a current of 500  $\mu$ A, with a set frame rate of 7.57 and average 5 frames per image. This

generated 3,137 images and a voxel size of 85.72  $\mu$ m. This specimen has been virtually reconstructed with MIMICS 20.0 (Materialise’s Interactive Medical Image Control System) software (Materialise Inc.; proprietary software at the Muséum national d’Histoire naturelle [MNHN], Paris, France) at the Atelier 3D, Centre de Recherche en Paléontologie – Paris (CR2P), MNHN, Paris. In addition to the 3D-model available as Supplementary Data 1, the outer surface of IRSNB P 9956 can be viewed via the RBINS Virtual Collections Platform (<http://virtualcollections.naturalsciences.be/>). The primary scanning data and the set of Y slices are stored on Belspo’s LTP platform (long-term preservation platform of the Belgian Federal Science Policy Office) and can be consulted upon request to the RBINS paleontology collection manager.

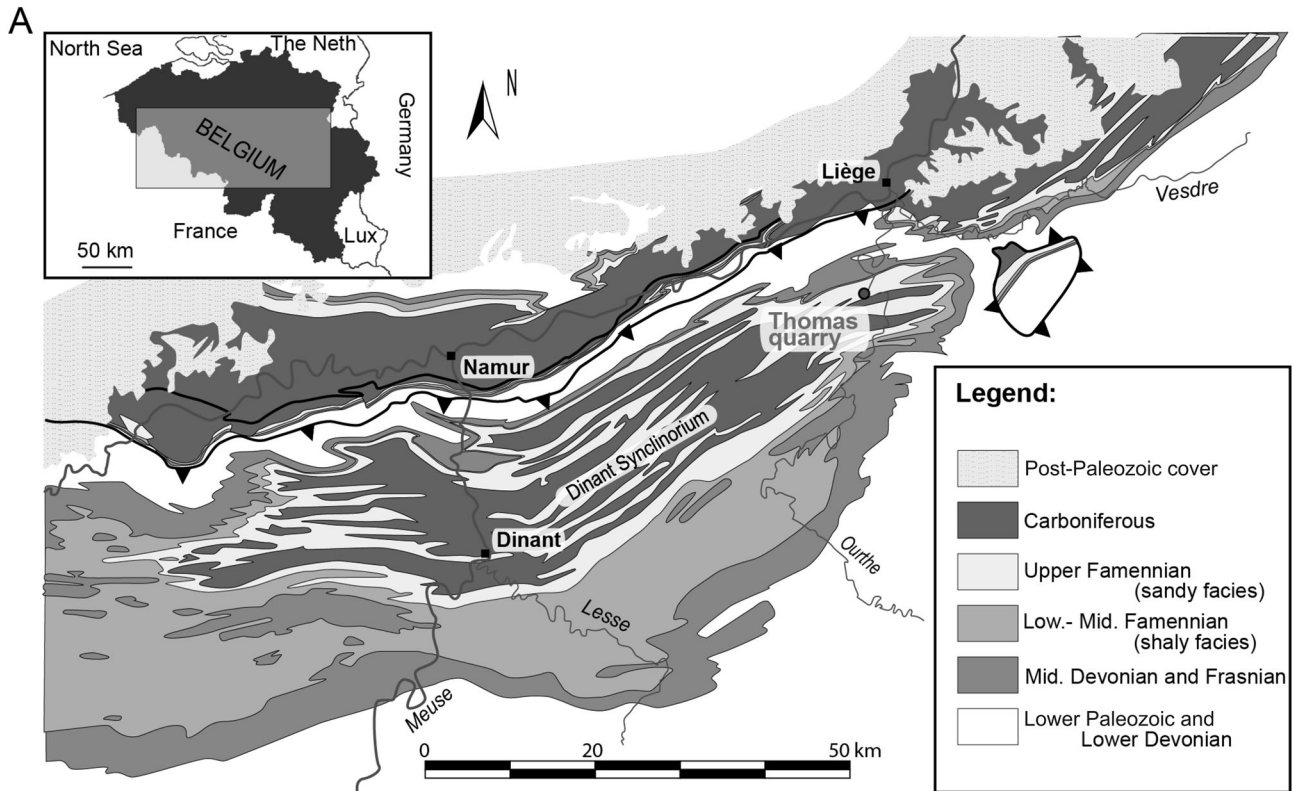
## SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880  
Subclass ELASMOBRANCHII Bonaparte, 1838  
Order CTENACANTHIFORMES Glikman, 1964  
Family CTENACANTHIDAE Dean, 1909  
cf. CTENACANTHIDAE

The studied specimen (IRSNB P 9956, old number: A9810) is flattened, although its anterior part curves slightly medially. It is then exposed in lateral view (Fig. 2A). Due to the poor preservation, it is difficult to observe any important features. The preserved fragment is 8.5 cm high and almost 22.5 cm long. The posterior part is the highest, tapering towards the anterior part. The anteriormost part is broken. A fossa is present on the posterolaterodorsal surface, probably representing an articular cotylus for the attachment with the palatoquadrate. The medial mandibular knob (mk) is not preserved, but part of a retroarticular process posterior to the cotylus is present. On the lingual surface (Fig. 2C) no notable features such as pits for tooth families, or a dental sulcus, or a symphyseal attachment area, are visible. Also, on the lateral surface we are not able to notice a ventral mandibular ridge extending from the articular cotylus.

## DISCUSSION AND CONCLUSIONS

Comparing the overall morphology and size of the described specimen with other, contemporary specimens: protacrodonts, stethacanthids, phoeobodonts (e.g., Ginter et al., 2010), the only group that matches the external features of this specimen are ctenacanthids. *Cladodus elegans* (Ginter and Maisey, 2007: text-fig. 3), for instance, shows a similar high posterior part of the Meckel’s cartilage that tapers anteriorly. In addition, the palatoquadrate attachment in *Cladodus elegans* appears to be anterior to the retroarticular process, as in the specimen described here. However, unlike our specimen, in *Cladodus elegans* there is no socket on the external surface of Meckel’s ramus. Hodnett et al. (2021: fig. 10C–F) presented four different Meckel’s cartilages of ctenacanthid sharks. The ctenacanth from Bear Gulch (CM 46006; Hodnett et al., 2021: fig. 10C) represents a more homogeneous and straight lower jaw than our specimen. The Meckel’s cartilage of *Heslerodus divergens* Trauttschold, 1879 (Hodnett et al., 2021: fig. 10D) shows a much more varied and irregular dorsal edge. The Belgian lower jaw is more delicate and elongated, than that of the Manzano ctenacanth (NMMNH P-68537; Hodnett et al., 2021: fig. 10E), in which the general outline is more rectangular, with roughly the same height throughout the whole specimen. The specimen that most closely resembles the specimen described here is *Ctenacanthus* sp. (CMNH 9450) from the Cleveland Shale, Ohio (Hodnett et al., 2021: fig. 10F), which shows a similar overall morphology and a retroarticular process posterior to the articular cotylus. Although *Ctenacanthus* sp. and the specimens studied here



Chrono-stratigraphy	Biostratigraphy		Dinant Synclinorium	
	spores	conodonts	SSW	NNE
Latest Famennian (Strunian)	LN	U		
	LE	praesulcata	ETROEUNGT	COMBLAIN-AU-PONT
	LL	L		
Late Famennian	VH	expansa	Epinette	Crupet
	VCo	M	Beverire	EVIEUX
		L		Royseux
	GF	U		
		L	trachytera	CINEY
	Mid Famennian	U+		SAINS
U		marginifera		SVP
L			AYE	ESNEUX
Early Famennian	GH	U		
		L	rhomboidea	
	U+			
	M	crepida	SAINS	FAMENNE
		L		
		U		
		M		
		L		

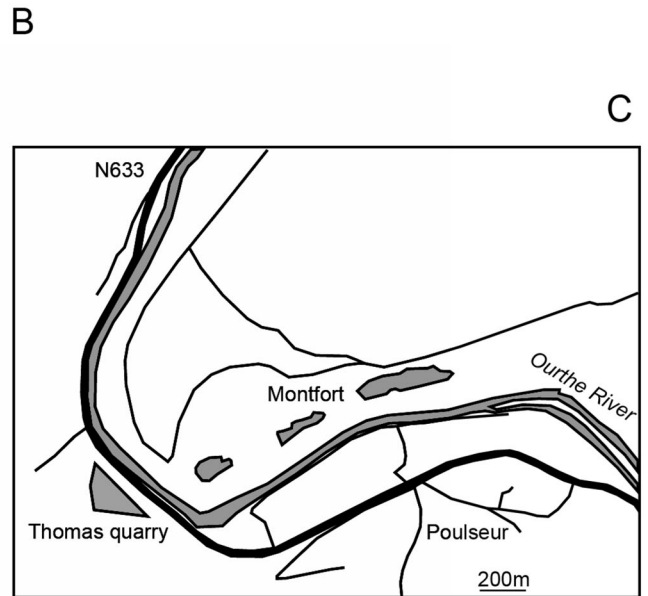


FIGURE 1. Geographic and geological context. **A**, Geological map of southern Belgium with the location of the Thomas quarry (modified from Denayer et al., 2016); **B**, general stratigraphic framework of the Famennian succession in the Dinant Synclinorium. Names in capital letters: formations, other names: members. Vertical dotted line corresponds to the stratigraphic interval of the Thomas quarry (modified from Denayer et al., 2016); **C**, road map of the Thomas quarry area. **Abbreviations:** CBL-LA-TOUR, Comblain-La-Tour Formation; GF, *Grandispora gracilis* – *Grandispora famenensis* zone; GH, *Grandispora gracilis* – *Acanthotriletes hirtus* zone; L, M, U, U+, lower, middle, upper and uppermost conodont zones; LE, *Retispora lepidophyta* – *Indotriradites explanatus* zone; LL, *Retispora lepidophyta* – *Knoxisporites literatus* zone; LN, *Retispora lepidophyta* – *Verucosisporites nitidus* zone; low, lower; Lux, Luxembourg; mid, middle; The Neth, the Netherlands; SVP, Souverain-Pré Formation; VCo, *Diducites versabilis* – *Grandispora cornuta* zone; VH, *Apiculiretusispora verrucosa* – *Vallatisporites hystricosus* zone.

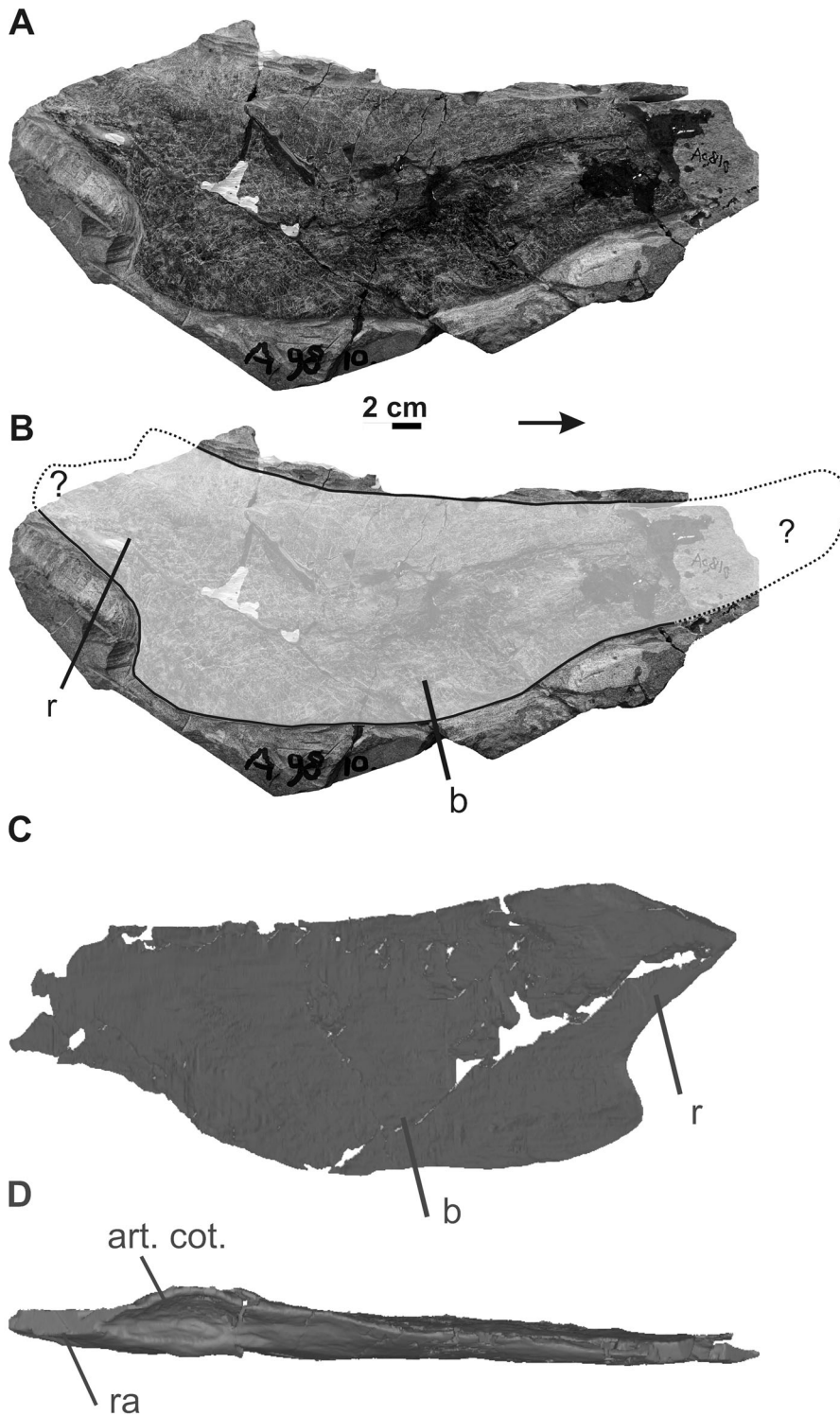


FIGURE 2. cf. Ctenacanthidae IRSNB P 9956. **A**, Right Meckel's cartilage exposed in lateral view; **B**, outline of the original (likely) shape of the cartilage; **C**, lingual view; **D**, dorsal view; see supplementary file for 3D model. **Abbreviations:** art. cot., articular cotylus; b, body; r, ramus; ra, retroarticular process.

look very similar, we cannot clearly state that they belong to the same genus due to the lack of distinctive features in our specimen. Based only on the general outline of the jaw we can probably assume that it belongs to the Ctenacanthidae family.

In this paper we presented the first occurrence of a fossilized cartilage element (right Meckel's cartilage) of a chondrichthyan from the Upper Devonian (Famennian) of continental Europe. Due to the poor state of preservation and lack of teeth in the

examined material, it is impossible to identify the specimen very precisely.

Taking into account the proportions of the body found in the articulated specimens e.g., in *Symmorium* from the Late Devonian of Morocco (Frey et al., 2020), it follows that the Meckel's cartilage occupies 1/8 of the length of the entire body. Then, the estimated total length of our individual would be 1.80 m.

## ACKNOWLEDGMENTS

The authors thank Editor C. Burrow and anonymous reviewers for many valuable remarks and kind revision of the early version of the manuscript. We are indebted to the “Ardenne research group” and to C. Mancini, worker at the “Thomas quarry” at that time and now manager. We thank the RBINS for facilitating access to their micro-CT scanner as part of the DiSSCo-Fed project and S. Goolaerts (RBINS) for operating the micro-CT. We acknowledge J. Denayer (Université de Liège) for his remarks regarding the geological framework as well as A. Folie and C. Cousin (RBINS) for the curatorial support, and R. Dearden (MNHN) for anatomical discussions. This paper benefited from funding supplied by the Belgian Science Policy Office (Belspo), and in particular of the Belspo-funded B2/202/P1/VERTIGO (S.O.) project, of which this paper is an official outcome. The final editorial work was supported by the PGI-NRI statutory funds (Project No 62.9012.2105.00.0).

## ORCID

Olga Wilk  <http://orcid.org/0000-0002-6199-4518>  
 Sebastien Olive  <http://orcid.org/0000-0001-9690-7464>  
 Alan Pradel  <http://orcid.org/0000-0002-7877-6306>  
 Jan L. Den Blaauwen  <http://orcid.org/0000-0002-3042-5494>  
 Piotr Szrek  <http://orcid.org/0000-0001-9855-2003>

## LITERATURE CITED

- Andreev, P. S., M. I. Coates, V. Karatajūtė-Talimaa, R. M. Shelton, P. R. Cooper, and I. J. Sansom. 2016a. *Elegestolepis* and its kin, the earliest monodontode chondrichthyans. *Journal of Vertebrate Paleontology*, 37:e1245664. DOI: [10.1080/02724634.2017.1245664](https://doi.org/10.1080/02724634.2017.1245664).
- Andreev, P. S., M. I. Coates, V. Karatajūtė-Talimaa, R. M. Shelton, P. R. Cooper, N. Z. Wang, and I. J. Sansom. 2016b. The systematics of the Mongolepidida (Chondrichthyes) and the Ordovician origins of the clade. *PeerJ*, 4:e1850. DOI: [10.7717/peerj.1850](https://doi.org/10.7717/peerj.1850).
- Benton, M. J. 2005. *Vertebrate Paleontology*. Blackwell Publishing, Oxford, 467 pp.
- Blieck, A., and H. Lelièvre. 1995. Palaeozoic vertebrates of northern France and Belgium. Part I: Heterostraci; Osteostraci; Thelodonti; Placodermi (Devonian). *Geobios* 28:311–317.
- Bonaparte, C. L. 1838. Synopsis vertebratorum systematis. *Nuovi Annali delle Scienze Naturali*. Bologna 2:105–133.
- Burrow, C. S., Turner, J. G. Maisey, S. Desbiens, and R. F. Miller. 2017. Spines of the stem chondrichthyan *Doliodus latispinosus* (Whiteaves) comb. nov. from the Lower Devonian of eastern Canada. *Canadian Journal of Earth Sciences* 54:1248–1262.
- Claypole, E. W. 1893. III—The Upper Devonian Fishes of Ohio. *Geological Magazine* 10:443–448.
- Clément, G. 2002. Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the late Famennian Evieux Formation of Belgium. *Palaeontology* 45:577–593.
- Clément, G., P. E. Ahlberg, A. Blieck, H. Blom, J. A. Clack, E. Poty, J. Thorez, and P. Janvier. 2004. Palaeogeography: Devonian tetrapod from western Europe. *Nature* 427:412–413.
- Cloutier, R., and A. M. Candilier. 1995. Palaeozoic vertebrates of northern France and Belgium: Part III—Sarcopterygii (Devonian to Carboniferous). *Geobios* 28:335–341.
- Coates, M. I., J. A. Finarelli, I. J. Sansom, P. S. Andreev, K. E. Criswell, K. Tietjen, M. L. Rivers, and P. J. La Riviere. 2018. An early chondrichthyan and the evolutionary assembly of a shark body plan. *Proceedings of the Royal Society B: Biological Sciences* 285:20172418.
- Dean, B., 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoirs of the American Museum of Natural History* 9:211–287.
- Denayer, J., C. Prestianni, P. Gueriau, S. Olive, and G. Clement. 2016. Stratigraphy and depositional environments of the late Famennian (Late Devonian) of Southern Belgium and characterization of the Strud locality. *Geological Magazine* 153:112–127.
- Derycke, C., and G. Clement. 2013. First assemblage of acanthodian scales and spines from the Famennian (Upper Devonian) of Durnal (Belgium), palaeobiogeographical and palaeoenvironmental implications. *Geologica Belgica* 16:18–26.
- Derycke, C., R. Cloutier, and A. M. Candilier. 1995. Palaeozoic vertebrates of northern France and Belgium: Part II - Chondrichthyes, Acanthodii, Actinopterygii (uppermost Silurian to Carboniferous). *Geobios* 19:343–350.
- Derycke, C., S. Olive, E. Groessens, and D. Goujet. 2014. Paleogeographical and paleoecological constraints on Paleozoic vertebrates (chondrichthyans and placoderms) in the Ardenne Massif: shark radiations in the Famennian on both sides of the Palaeoethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414:61–67.
- Derycke-Khatir, C. 1994. *Microrestes de vertébrés du paléozoïque supérieur de la Manche au Rhin: Biodiversité -Biostratigraphie -Biogéographie*. Doctoral thesis, Université des Sciences et Technologies de Lille, 248 pp.
- Frey, L., M. I. Coates, K. Tietjen, M. Rücklin, and C. Klug. 2020. A symmoriiform from the Late Devonian of Morocco demonstrates a derived jaw function in ancient chondrichthyans. *Communications Biology* 3(1):1–10.
- Ginter, M., and J. G. Maisey. 2007. The braincase and jaws of *Cladodus* from the Lower Carboniferous of Scotland. *Palaeontology* 50:305–322.
- Ginter, M., S. Gouwy, and S. Goolaerts. 2017. A classic Late Frasnian (Devonian) chondrichthyan assemblage from southern Belgium. *Acta Geologica Polonica* 67:381–392.
- Ginter, M., O. Hampe, C. J. Duffin, and H. P. Schultze. 2010. *Handbook of Paleichthyology*. Volume 3D. Chondrichthyes. Paleozoic Elasmobranchii: Teeth. Verlag Dr Friedrich Pfeil, München, 168 pp.
- Glikman, L.S. 1964. [Sharks of the Paleogene and their stratigraphic significance]. Moscow, Nauka Press, 229 pp. [in Russian].
- Gross, W. 1965. Über die Placodermen-Gattungen *Asterolepis* und *Tiaraspis* aus dem Devon Belgiens und einen fraglichen *Tiaraspis*-Rest aus dem Devon Spitzbergens. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 41(16):1–19.
- Harris, J. E. 1938. The neurocranium and jaws of *Cladoseleche*. *Scientific Publications*. Cleveland Museum of Natural History 8:7–12.
- Hodnett, J. P. M., E. D. Grogan, R. Lund, S. G. Lucas, T. Suazo, D. K. Elliott, and J. Pruitt. 2021. Ctenacanthiform sharks from the Late Pennsylvanian (Missourian) Tinajas Member of the Atrasado Formation, central New Mexico; pp. 391–424 in S. G. Lucas, W. A. Dimichele, and B. D. Allen (eds.), *Kinney Brick Quarry Lagerstätte*. New Mexico Museum of Natural History and Science Bulletin 84.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880:649–662.
- Janvier, P., and G. Clément. 2005. A new groenlandaspidid arthrodire (Vertebrata: Placodermi) from the Famennian of Belgium. *Geologica Belgica* 8:51–67.
- Janvier, P., and P. Racheboeuf. 2018. The Palaeozoic vertebrates of Bolivia, with comments on the faunal and environmental context of the ‘Malvinokaffric realm’. *Fósiles y facies de Bolivia* 22–35.
- Janvier, P., and M. Suarez-Riglos. 1986. The Silurian and Devonian vertebrates of Bolivia. *Bulletin de l'Institut français d'études andines* 15:73–114.
- Johanson, Z., M. Tanaka, N. Chaplin, and M. Smith, M. 2008. Early Palaeozoic dentine and patterned scales in the embryonic catshark tail. *Biology Letters* 4:87–90.
- Lelièvre, H. 1982. *Ardennosteus ubaghisi* n. g. n. sp. Brachythoraci primitif (vertébré, placoderme) du Famennien d'Esneux (Belgique). *Annales de la Société Géologique de Belgique* 105:1–7.
- Long, J. A., C. J. Burrow, M. Ginter, J. G. Maisey, K. M. Trinajstić, M. I. Coates, G. C. Young, and T. J. Senden. 2015. First shark from the Late Devonian (Frasnian) Gogo Formation, Western Australia sheds new light on the development of tessellated calcified cartilage. *PLoS One* 10(5):1–24.
- Lund, R. 1974. *Stethacanthus altonensis* (Elasmobranchii) from the Bear Gulch Limestone of Montana. *Annals of the Carnegie Museum* 45:161–178.
- Maisey, J. G. 1989. *Hamiltonichthys mapesi*, g. and sp. nov. (Chondrichthyes, Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates* 2931:1–42.

- Maisey, J. G. 2001. A primitive chondrichthyan braincase from the Middle Devonian of Bolivia. *Systematics Association Special Volume* 61:263–288.
- Maisey, J. G., and M. E. Anderson. 2001. A primitive chondrichthyan braincase from the Early Devonian of South Africa. *Journal of Vertebrate Paleontology* 21:702–713.
- Maisey J.G., P. Janvier, A. Pradel, J. S. S. Denton, A. Bronson, R. Miller, and C. J. Burrow. 2019. *Doliodus* and pucapampellids. Contrasting perspectives on stem chondrichthyan morphology; pp. 87–109 in Z. Johanson, C. Underwood, and M. Richter (eds.), *Evolution and Development of Fishes*. Cambridge University Press.
- Miller, R. F., R. Cloutier, and S. Turner. 2003. Oldest articulated chondrichthyan from the Early Devonian period. *Nature* 425:501–504.
- Newberry, J. S. 1889. *The Paleozoic Fishes of North America*. United States Geological Survey Monograph, 340 pp.
- Olive, S. 2015. Devonian antiarch placoderms from Belgium revisited. *Acta Palaeontologica Polonica* 60:711–731.
- Olive, S., G. Clément, E. B. Daeschler, and V. Dupret. 2015a. Characterization of the placoderm (Gnathostomata) assemblage from the tetrapod-bearing locality of Strud (Belgium, upper Famennian). *Palaeontology* 58:981–1002.
- Olive, S., Y. Leroy, E. B. Daeschler, J. P. Downs, S. Ladevèze, and G. Clément. 2020. Tristichopterids (Sarcopterygii, Tetrapodomorpha) from the Upper Devonian tetrapod-bearing locality of Strud (Belgium, upper Famennian), with phylogenetic and paleobiogeographic considerations. *Journal of Vertebrate Paleontology* 40: e1768105.
- Olive, S., G. Clément, J. Denayer, C. Derycke, V. Dupret, P. Gerrienne, P. Gueriau, J. M. Marion, B. Mottequin, C. Prestianni. 2015b. Flora and fauna from a new Famennian (Upper Devonian) locality at Becco, eastern Belgium. *Geologica Belgica* 18:92–101.
- Pradel, A., J. G. Maisey, P. Tafforeau, and P. Janvier. 2009. An enigmatic gnathostome vertebrate skull from the Middle Devonian of Bolivia. *Acta Zoologica* 90:123–133.
- Pradel, A., J. G. Maisey, P. Tafforeau, R. H. Mapes, and J. Mallatt. 2014. A Palaeozoic shark with osteichthyan-like branchial arches. *Nature* 509:608–611.
- Sansom, I. J., M. M. Smith, and M. P. Smith. 1996. Scales of thelodont and shark-like fishes from the Ordovician of Colorado. *Nature* 379:628–630.
- Sansom, I. J., N. S. Davies, M. I. Coates, R. S. Nicoll, and A. Ritchie. 2012. Chondrichthyan-like scales from the Middle Ordovician of Australia. *Palaeontology* 55:243–247.
- Thorez, J., and R. Dreesen. 1986. A model of a regressive depositional system around the Old Red Continent as exemplified by a field trip in the Upper Famennian “Psammites du Condroz” in Belgium. *Annales de la Société géologique de Belgique* 109:285–323.
- Thorez, J., and R. Dreesen. 2002. The Condroz Sandstone Group (Upper Famennian) revisited. *Geologica Belgica Intern. Meeting*, 11–15 September 2002, Field Trip Guidebook.
- Thorez, J., R. Dreesen, and M. Streel. 2006. Famennian. *Geologica Belgica* 9:27–45.
- Thorez, J., E. Goemaere, and R. Dreesen. 1988. Tide- and wave-influenced depositional environments in the Psammites du Condroz (Upper Famennian) in Belgium; pp. 389–415 in De Boer et al. (eds.) *Tide-influenced sedimentary environments and facies*, Dordrecht: D. Reidel Publishing Company.
- Thorez, J., M. Streel, J. Bouckaert, and M. J. M. Bless. 1977. Stratigraphie et paléogéographie de la partie orientale du Synclinorium de Dinant (Belgique) au Famennien Supérieur: un modèle de bassin sédimentaire reconstitué par analyse pluridisciplinaire sédimentologique et micropaléontologique. *Mededelingen-Rijks Geologische Dienst* 28:17–32.
- Tomita, T. 2015. Pectoral fin of the Paleozoic shark, *Cladoselache*: new reconstruction based on a near-complete specimen. *Journal of Vertebrate Paleontology*, 35:e973029. DOI: 10.1080/02724634.2015.973029.
- Trautschold, H. 1879. Die Kalkbrüche von Mjatschkowa. Eine Monographie des oberen Bergkalks. *Nouveau Mémoires de la Société Impériale des Naturalistes de Moscou* 14:3–82.
- Williams, M. 1985. Cladodont-level sharks from the Upper Devonian Cleveland Shale. *Palaeontographica* 190:83–158.
- Williams, M. E. 1998. A new specimen of *Tamiobatis vetustus* (Chondrichthyes, Ctenacanthoidea) from the late Devonian Cleveland Shale of Ohio. *Journal of Vertebrate Paleontology* 18:251–260.
- Yazdi, M., and S. Turner. 2000. Late Devonian and Carboniferous vertebrates from the Shishtu and Sardar formations of the Shotori Range, Iran. *Records of the Western Australian Museum, Supplement* 58:223–240.
- Young, G. C. 1997. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *Journal of Vertebrate Paleontology* 17(1):1–25. DOI:10.1080/02724634.1997.10010948.
- Zangerl, R. 1981. Chondrichthyes I: Paleozoic Elasmobranchii; in H.-P. Schultze (ed.), *Handbook of Paleichthyology*, Volume 3A. Verlag Dr. Friedrich Pfeil, München, 116pp.
- Zhu, M., X. Yu, P. E. Ahlberg, B. Choo, J. Lu, T. Qiao, Q. Qingming, W. Zhao, L. Jia, H. Blom, and Y. A. Zhu. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* 502:188–193.

Submitted February 12, 2021; revisions received July 6, 2021;

accepted July 8, 2021.

Handling Editor: Carole Burrow.