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SHORT COMMUNICATION

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

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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; Claypole, 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; Blieck 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 (fluviolagunal 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

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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 Buisonjé, 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) with a copper filter. Images were generated at a voltage of 150 kV and a current of 500 μA, 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 μm. 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 symphysial 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, phoebodonts (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* Trautschold, 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

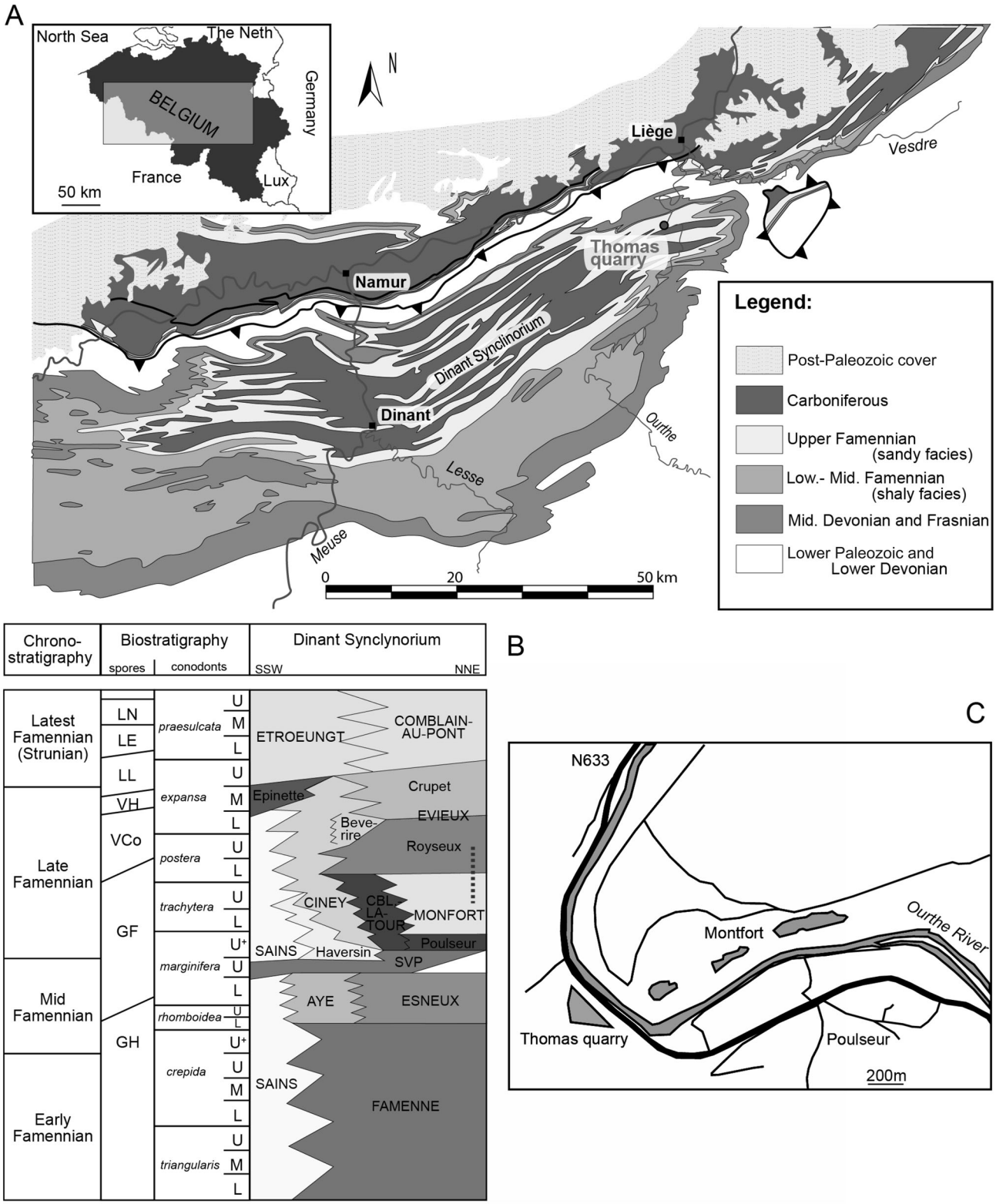

FIGURE 1. Geographic and geological context. **A**, Geological map of southern Belgium with the location of the Thomas quarry (modified from Denayer et al., 2016); **B**, general stratigraphic framework of the Famennian succession in the Dinant Synclinorium. Names in capital letters: formations, other 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 – Verrucosisporites 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.

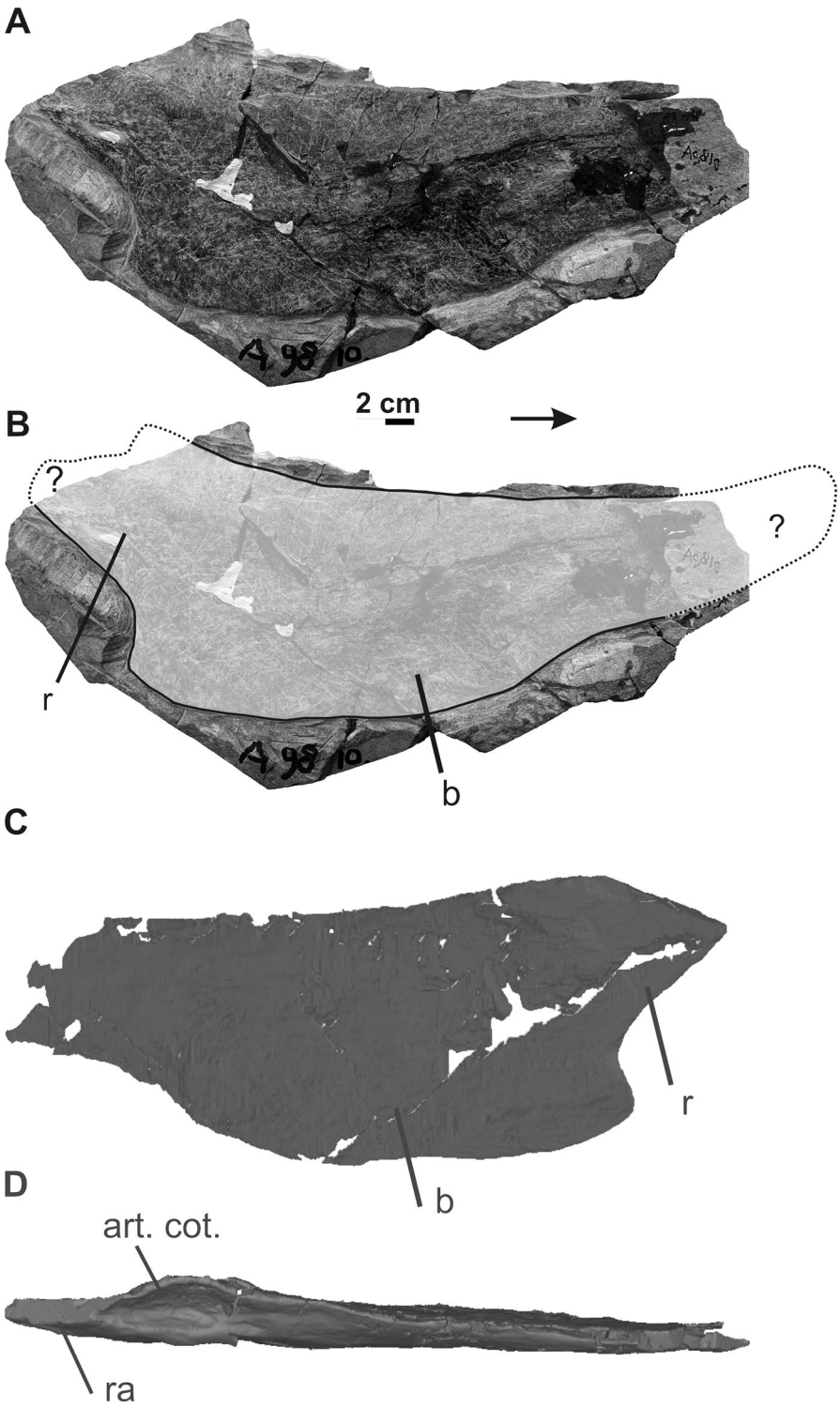

FIGURE 2. cf. Ctenacanthidae IRSNB P 9956. **A**, Right Meckel's cartilage exposed in lateral view; **B**, outline of the original (likely) shape of the cartilage; **C**, lingual view; **D**, dorsal view; see supplementary file for 3D model. **Abbreviations: art. cot.**, articular cotylus; **b**, body;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

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