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A new callorhinchid genus (Holocephali, Chimaeroidei) from the early Bajocian of Ottange-Rumelange, on the Luxembourg-French border

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Abstract. An incomplete chimaeroid (Holocephali, Chimaeroidei) mandibular dental plate from the early Bajocian (*Humphriesianum* Zone) of Ottange-Rumelange, on the Luxembourg-French border, is described as a new genus and species of callorhinchid fish *Ottangodus lotharingiae* gen. et sp. nov. Comparison of the described plate with other Jurassic chimaeriform fish (both myricanthid and chimaeroid) mandibular plates shows relationships with callorhinchids and in turn close relationships with the genus *Pachymylus* Woodward, known from the Callovian of England. The plate of the new genus shows a set of primitive characters for chimaeroids (very high descending lamina, low oral part of the plate, large centrally placed median tritor occupying most of the oral part of the plate and an absence of mesio-labial system of the tritors) and could thus belong to a basal Chimaeroidei taxon. This is the first record of the Chimaeroidei from the Jurassic of Lorraine and the fourth chimaeriform genus known from the Mesozoic of the region.

Key words: Callorhinchidae, Chimaeriformes, Lorraine, mandibular tooth plate, Middle Jurassic, new genus

Introduction

Chimaeroid fishes of the suborder Chimaeroidei are a small group of holocephalian cartilaginous fishes (Holocephali), represented in the Recent fauna by 3 families, 6 genera and 51 species (Didier, 1995, 2004; Web-project 'Catalogue of Life', www.catalogueoflife.org), which inhabit mainly deep waters (rhinochimaerids, chimaerids) with a small number of species present in near-shore environments (callorhinchids). In contrast to this, fossil Chimaeroidei had a broad distribution within the shallow epicontinental seas of Europe during the Jurassic, Cretaceous and Paleogene (Nessov and Averianov, 1996; Stahl, 1999).

Chimaeroid fishes have continuously growing dental plates (statodont dentition *sensu* Patterson, 1992), in contrast to the continual replacement of teeth in elasmobranchs (lyodont dentition; see also Stahl, 1999). It is these isolated tooth plates that form the principal fossil chimaeroid material (two tooth plate pairs in the upper jaw—vomerine and palatine plates; one pair in the lower jaw—mandibular plates); rarer are fin spines and frontal claspers, whilst egg case imprints and partial/complete skeletons (Late Jurassic, Germany; Late Cretaceous, Lebanon and England; see Stahl, 1999 for a review) are extremely rare.

The earliest fossil chimaeroid fishes are from the European Early Jurassic and consist of a single tooth plate from the Pliensbachian of south England (*Eomanodon simmsi* Ward and Duffin, 1989) and two records from SW Germany: an associated lower dentition of *Brachymylus latus* Duffin, 1996 from the Pliensbachian of Bavaria and a single plate of *Bathytheristes gracilis* Duffin, 1995 from the early Toarcian of Ohmden, Baden-Württemberg. The description of late Carnian (late Triassic) rhinochimaeroid-type egg case imprints from Yakutia, in the Far East of Russia (Vozin, 1968) as well as the recent discovery of a callorhinchid-type egg case imprint from the Late Triassic (late Norian or Rhaetian) of New Zealand (Gottfried and Fordyce, 2015) show that the earliest chimaeroid fishes had a global distribution as early as the Late Triassic and these data also show an early divergence of the callorhinchid and rhinochimaerid lineages.

The oldest recorded diverse chimaeroid assemblage including at least several species is known from the Aalenian (Middle Jurassic) of Württemberg, SW Germany (Quenstedt, 1858; Riess, 1887; Jaekel, 1901). It consists of several "toothplate" species (*Ischyodus personati* (Quenstedt, 1852), *I. aalensis* (Quenstedt, 1852) and several others) as well as ichnospecies *"Callorhinchus" germanicus* (Brown, 1946) based on several egg case imprints. This assemblage was reported initially as being Bajocian in age (Stahl, 1999) but in fact, most known chimaeroid material was collected in the stratotypic Aalenian area (Dietl and Etzold, 1977).

At the moment, 42 nominal chimaeroid species have been described from the European Jurassic (Stahl, 1999; Popov, 2003) belonging to the following genera: *Ischyodus* Egerton, 1843 (with 23 nominal species), *Brachymylus* Woodward, 1892 (4), *Duffinodus* Popov, 2003 (1), *Pachymylus* Woodward, 1892 (1), *Elasmodectes* /'*Ganodus*' group (7), *Eomanodon* Ward and Duffin, 1989 (1), *Bathytheristes* Duffin, 1996 (1), *Callorhinchus* Lacépède, 1798 (2 egg case species) and *Harriotta* Goode and Bean, 1895 (2 egg case species). Most of these species were recorded from the Bathonian (11 nominal species), Tithonian (10), Kimmeridgian (8) and the Callovian-Oxfordian interval (3).

Bajocian chimaeroid records are relatively sparse and consist of a small number of tooth plates. One of them, represented by a single figured specimen, represents *Ischyodus bifurcati* Quenstedt, 1883, a species from the German (Württemberg) 'Hohenzollern bei Hechingen' locality (Dogger delta). This species was based on a single unnumbered specimen (Tübingen University collection), consisting of a rounded piece of laminated pleromin from the symphyseal tritor of the mandibular plate of *Ischyodus* sp.; therefore it represents a *nomen dubium*, as the type specimen has no diagnostic characters (E.V.P., personal observation, 2008). An additional unpublished French Bajocian (?) record is a palatine dental plate of *Pachymylus* sp. (the plate is typical for the genus and possesses only a moderate inner tritor), deposited in the Le Havre Natural History Museum, France under the number MNBO 1318 (E.V.P., personal observation, 2007).

Because of this poor Bajocian chimaeroid record, any material from this time interval is of great interest. The aim of this paper is to record a new chimaeroid dental plate from Cimalux quarry (formerly Intermoselle) near the towns of Ottange and Rumelange, on the Luxembourg-French border (Figure 1A, B). Despite the incompleteness of the plate, it shows characters sufficient for the reconstruction of the missing part of the plate, the proposal of a suitable diagnosis and comparison with other Jurassic holocephalians.

This is the first record of Jurassic Chimaeroidei remains and the fourth chimaeriform (Chimaeriformes) genus known to date from the France-Luxembourg-Belgium Lorraine. The only other chimaeriforms described earlier from the region are all myriacanthoid fishes (Myriacanthoidei): an isolated tooth plate of *Halonodon luxembourgensis* Duffin and Delsate, 1993 from the Early Jurassic (Hettangian, *Angulata* Zone) of Brouch (Duffin and Delsate, 1993) in the Luxembourg Lorraine, a plate of *Myriacanthus paradoxus* Agassiz, 1836 from the Early Jurassic (Sinemurian) of Clairefontaine near Arlon in the Belgian Lorraine (Duffin and Delsate, 1995), and some plates of *Chimaeropsis foussi* Casier, 1959 and *Halonodon warneri* Duffin, 1984 from the Early Jurassic (Sinemurian) of Huombois near Virton in the Belgian Lorraine (Casier, 1959; Duffin, 1984).

The plate described herein is housed in the Musée National d'Histoire Naturelle de Luxembourg collection together with other fish remains from the Cimalux Quarry. Other comparative chimaeroid dental plates figured and discussed in the text are deposited in other public collections (see below).

Geological setting

Hary (1970), Bintz *et al.* (1973) and, more recently, Lathuilière (2005) and Boulvain *et al.* (2017) have provided a lithostratigraphical log of the Cimalux Quarry (49°26′59″N, 5°59′18″E) between Ottange and Rumelange, close to the border between the Grand Duchy of Luxembourg and France. The Cimalux Quarry is a continuation of the now disused Weiss Kaul Quarry, and is worked by the Groupe Ciments Luxembourgeois. The quarry exposes four lithological units of carbonate rocks of lower Bajocian age (Figure 1C). The upper part of the section (level IV in the quarry) is formed by marls belonging to the 'Marnes sableuses d'Audun le Tiche' unit. These sediments are dated by the zonal ammonite *Stephanoceras humphriesianum* (Bintz *et al.*, 1973; Lathuilière, 2005). The palaeoenvironment corresponds to an open sea with an oxygenated bottom (Lathuilière, 2005).

The underlying marls between the reef bodies (Calcaires d'Audun le Tiche) have yielded a rather impoverished fauna with *Synechodus*, *Protospinax*, Orectolobiformes, actinopterygians cfr. Pachycormiformes and Pycnodontiformes. The alternating limestones and marls (Marnes sableuses d'Audun le Tiche) overlying the reef bodies yield a more abundant and diverse fauna (Fayard *et al.*, 2005). The marly layer IV/12 covers the shell breccia limestone IV/11 and is the most fossiliferous (Delsate and Felten, 2015), with actinopterygians (Lepisosteiformes, Pycnodontiformes, probable Pachycormiformes and Furidae), hybodontids (?*Hybodus* sp., *Acrodus* sp., "*Polyacrodus*" sp., *Lissodus* sp.), neoselachian sharks (*Synechodus levis*, *Synechodus* cf. *duffini*,

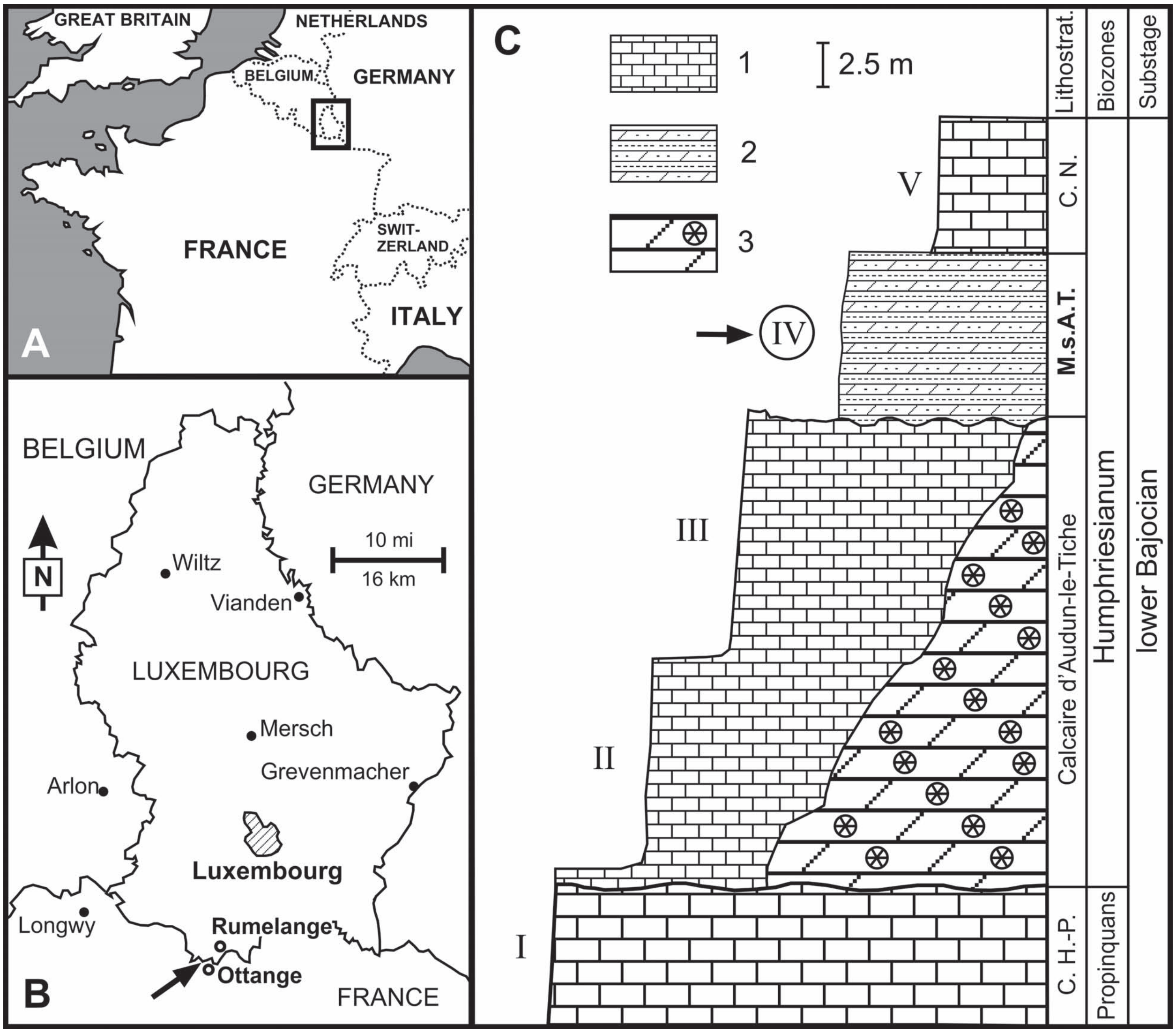

Figure 1. **A,** map showing the location of the Grand Duchy of Luxembourg in western Europe; **B,** detailed map of the region showing the location of the Cimalux Quarry (indicated by an arrow) between Ottange-Rumelange, on the Luxembourg-French border; **C,** stratigraphic log for the Cimalux Quarry. Symbols: 1, limestone; 2, marl; 3, bioherm. I–V, quarry levels. Level with fishes indicated by a horizontal arrow. Abbreviations of lithostratigraphy units: C.H-P. – Calcaire de Haut-Pont; M.s.A.T., Marnes sableuses d'Audun-le-Tiche; C.N., Calcaire de Nondkeil.

Paraorthacodus sp., *Pseudonotidanus* sp., *Sphenodus* cf. *longidens*, *Paracestracion* sp., *Protospinax magnus* and *P. bilobatus*, aff. *Palaeobrachaelurus* sp. and indeterminate orectolobiforms). The Holocephali are restricted to a single plate of *Ottangodus lotharingiae* gen. et sp. nov., described herein. Rare remains of marine reptiles are also present, represented by the ichthyosaur *Ophthalmosaurus* sp., plesiosaur remains and the crocodile *Steneosaurus* sp. A bone fragment from the same layer of the Cimalux Quarry, deposited in the private collection of the third author (RF) and reported earlier (Delsate and Felten, 2005, unnumbered figure on page 116) as a 'myriacanthid' tooth plate, is shown to be of non-fish origin (Delsate *et al.*, 2018) after careful reexamination by the authors.

The diverse and abundant shark and fish fauna from this layer is very similar to that of the British Bathonian (Underwood, 2004; Underwood and Ward, 2004), lacking the Carcharhiniformes and Batomorphi, but more diverse in synechodontiform sharks (Delsate and Felten, 2015).

Terminology

The descriptive terminology and measurements used here are based on the works of the first author (Popov, 1999, 2003, 2004; Popov and Beznosov, 2006; Popov and Efimov, 2012; Popov and Machalski, 2014); a key to the descriptive terms and measurements is given in Figures 2 and 4.

The morphological peculiarities of chimaeroid tooth plates are more easily assessed on the basis of the plate cross section. The cross section of the Belgian toothplate can be extrapolated from the reconstructed lingual view, showing the lingual expression of the form and thickness of the descending lamina and the form and distribution of hypermineralised pleromin bodies. The use of the lingual view (visible or reconstructed cross section) is informative for the interspecific comparison of chimaeroid plates, as it avoids affecting the results of individual wear of the occlusal surface and the intraspecific variability of tritoral pattern. The lingual part of chimaeroid dental plates, visible in lingual view, is often poorly preserved; thus, a partly reconstructed and composite analogue is the 'lingual cross section' used here. A simple case of the lingual cross section with no pleromin bodies shown was first used by Newton (1878, pl. I, fig. 7, pl. II, fig. 7, pl. VI, fig. 4) and more recently by Popov (2003) and Popov and Shapovalov (2007). For the reconstruction of the lingual cross section, all available morphological peculiarities of the studied plate are used (distribution of tritors visible in mesial view, occlusal tritoral pattern, form and distribution of other plate structures, etc.). Restored parts of the plate MnhnL BM 485, described below, are shown in Figure 2, whilst other holocephalian plates used for comparison are presented in Figure 4.

Institution abbreviations.—MnhnL, Luxembourg Natural History Museum, Luxembourg, Grand Duchy of Luxembourg; NHMUK, Natural History Museum, London, UK; SSU, Regional Museum of Physical Geography, Saratov State University, Saratov, Russia; IRSNB, Royal Institute of Natural Sciences, Brussels, Belgium; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SM, Sedgwick Museum of Earth Sciences, Cambridge University, UK; TU, Geological Museum, Tubingen University, Germany.

Systematic palaeontology

Higher-level taxonomy (superfamily and higher) follows Nelson (2006). The composition of the family Callorhinchidae Garman, 1901 is based on that of Popov (2003, 2004).

Class Chondrichthyes Huxley, 1880

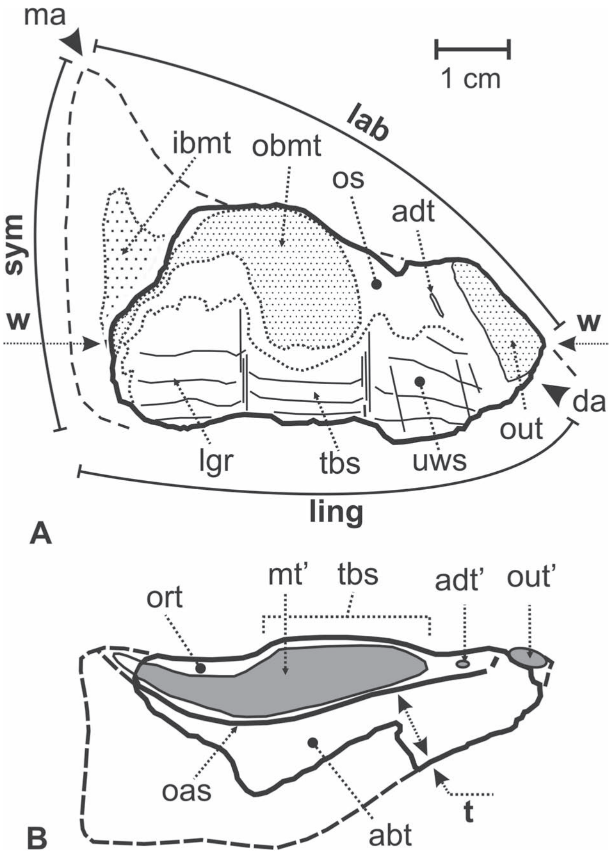

Figure 2. Morphological interpretation and applied terminology to the holotype MnhnL BM 485 *Ottangodus lotharingiae*, gen. et sp. nov., with reconstructed mesial part of the plate. **A,** occlusal view; **B,** lingual view. Abbreviations: abt, aboral region of the plate; adt, additional outer tritor; da, distal angle; ibmt, inner branch of the median tritor; lab, labial margin; lgr, lines of growth; ling, lingual margin; ma, mesial angle; mt, median tritor; oas, oral-aboral suture; obmt, outer branch of the median tritor; ort, oral region of the plate; os, occlusal surface sensu stricto; out, outer tritor; sym, symphyseal margin; t, maximum visible thickness of the lateral descending lamina; tbs, tritoral bolster; uws, unworn (post-occlusal) surface of occlusal surface sensu lato; w, width of the plate; mt', adt', out' etc., pleromin bodies of the corresponding tritors (in lingual cross section). Restored parts of the plate are shown by linear doted lines; dotted lines on the occlusal view mark the boundary between occlusal (os) and post-occlusal (uws) surfaces of the plate.

Subclass Holocephali Bonaparte, 1832
Superorder Holocephalomorpha Nelson, 2006
Order Chimaeriformes Obruchev, 1953
Suborder Chimaeroidei Patterson, 1965
Superfamily Callorhinchoidea Garman, 1901
Family Callorhinchidae Garman, 1901

Genus ***Ottangodus*** gen. nov.

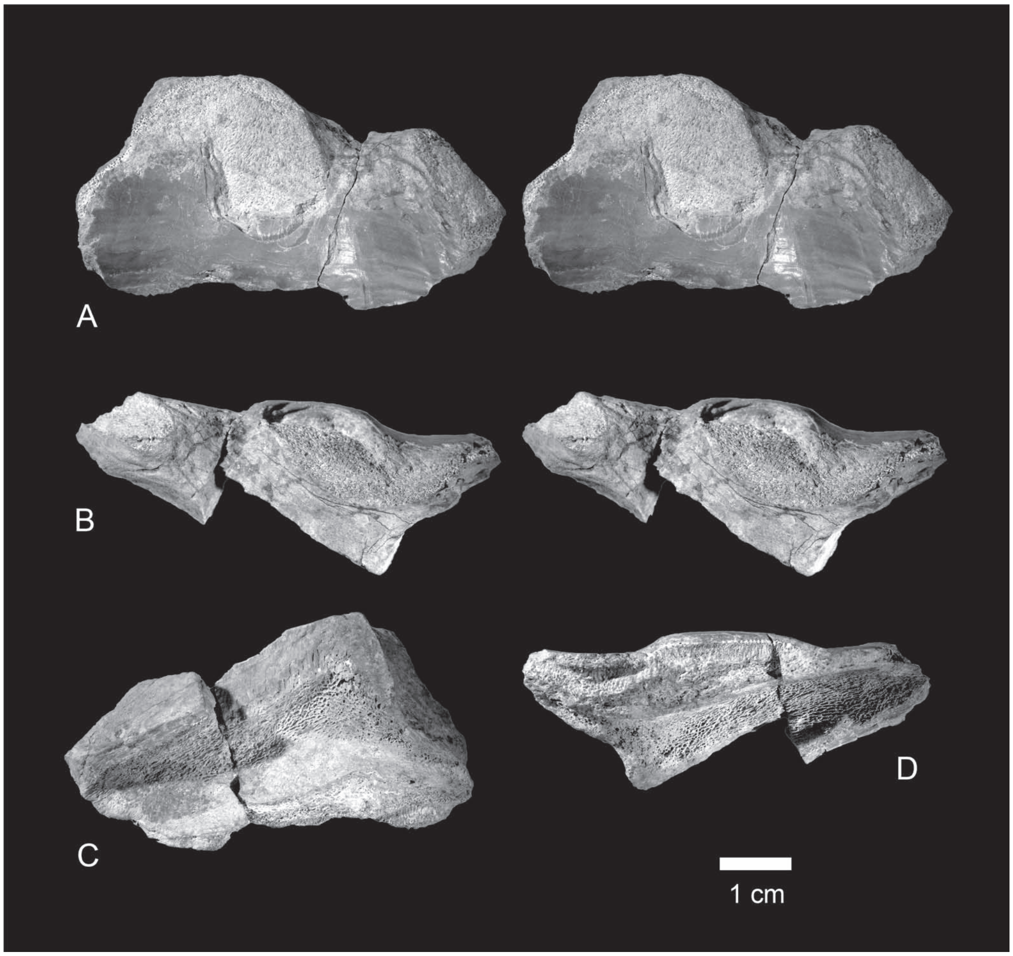

Figure 3. *Ottangodus lotharingiae*, gen. et sp. nov., holotype MnhnL BM 485, incomplete right mandibular plate. **A,** occlusal view (stereopair); **B,** labial view (stereopair); **C,** basal view; **D,** lingual view.

Type species.—*Ottangodus lotharingiae* gen. et sp. nov; by original designation.

Diagnosis.—A callorhinchid chimaeroid fish, known from the mandibular plate only. Mandibular plate with very high descending lamina, more than twice higher than the oral part of the plate. The oral region of the plate is fully occupied by vascular tritors: a laterally placed outer tritor and a large, centrally placed, median tritor. The median tritor is compound in cross-section and makes up most of the inner space of the oral region of the plate.

Etymology.—The genus is named after 'Ottange': a town in NE France where the holotype was collected and Greek 'odous': tooth. The name means 'tooth from Ottange'.

Ottangodus lotharingiae sp. nov.

Figures 2, 3, 4B

Callorhynchidae (Plaque dentaire de chimère). Delsate and Felten, 2005. p. 115, unnumbered figure.

Callorhinchidae indet. Delsate and Felten, 2015, p. 28, fig. 9F.

Type specimen.—Holotype MnhnL BM 485, incomplete right mandibular plate.

Diagnosis.—As for the genus.

Etymology.—Named after Latin '*Lotharingia*' referring to the region (Lorraine) where the holotype was collected.

Type locality.—Cimalux Quarry between Ottange (NE France) and Rumelange (Luxembourg); 49°27′4.32″N, 5°59′32.91″E.

Type horizon.—Marnes sableuses d'Audun le Tiche, *Stephanoceras humphriesianum* ammonite Zone, early Bajocian, Middle Jurassic.

Description.—The type specimen, MnhnL BM 485, consists of the distal part of a large right mandibular plate. The plate is broad and subtriangular in occlusal view; the maximum width (*w*) of the specimen is 50 mm. The plate

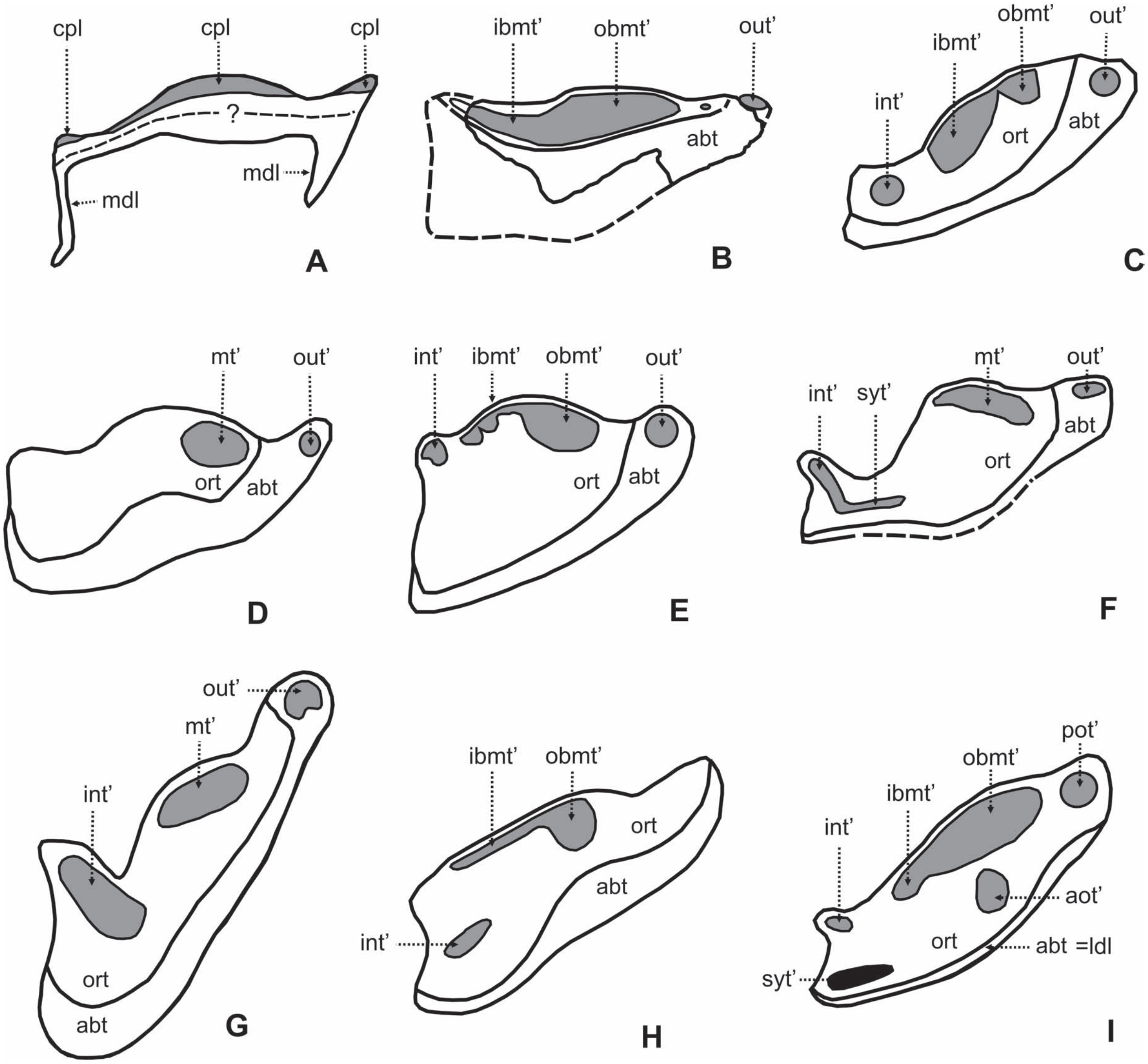

Figure 4. Comparisons of lingual cross sections of mandibular plates for different Jurassic chimaeriform fishes. **A,** myriacanthoid; **B–I**, chimaeroids; A, IRSNB P4529bis, holotype of *Halonodon warneri* Duffin, 1984, left plate (reversed), early Sinemurian, early Jurassic, Huombois, Belgium; B, MnhnL BM 485, *Ottangodus lotharingiae* gen. et sp. nov., incomplete right plate, early Bajocian, middle Jurassic, Ottange-Rumelange, Lorraine, NE France; C, SSU 155/65, *Callorhinchus* sp., right plate, middle Volgian substage, late Jurassic, Kuntzevo, Moscow, central Russia (from Popov and Shapovalov, 2007); D, BHNH P 6889, syntype of *Pachymylus leedsi* Woodward, 1892, right plate, Oxford Clay, Callovian, middle Jurassic, Peterborough, UK; E, SSU 155/29, holotype of *Duffinodus nikolaii* Popov, 2003, right plate, late Callovian, middle Jurassic, Dubki locality, Saratov, Russia (see Popov, 2003); F, BMNH P6891, holotype of *Brachymylus altidens* Woodward, 1892, left plate (reversed), Oxford Clay, Callovian, middle Jurassic, Peterborough, UK; G, BMNH P5141a, "*Brachymylus altidens"*, left plate (reversed) of associated dentition, Oxford Clay, Callovian, middle Jurassic, Peterborough, UK; H, SMNS 80008, "*Brachymylus*" *latus* Duffin, 1996, left plate of associated lower dentition (reversed), Pliensbachian, early Jurassic, Unterstürmig, Bavaria, Germany; I, SM J 29225, *Ischyodus egertoni* (Buckland, 1835), left plate (reversed), Kimmeridge Clay, Ely, Cambridgeshire, UK. Not to scale. All plates are oriented in life position of "open mouth", with the symphyseal surface to the left and by occlusal surface to the top. Vascular pleromin of tritoral bodies is shown as a grey fill, laminated pleromin as a black fill (I). For several specimens (A, C, E) coronal part of occlusal surfaces are partly restored. Restored parts of aboral region of the plates are shown by linear doted lines (B, F). Abbreviations (see Figure 2 and additionally): aot', pleromin body of the anterior outer tritor; cpl, coronal pleromin of myriacanthid plate organized in three occlusal tritors by sectorial wear; int', pleromin body of the inner tritor (in lingual view); mdl, descending lamina of 'myriacanthid' type; ldl, lateral descending lamina of 'chimaeroid' type; pot', pleromin body of the posterior outer tritor; syt', pleromin body of the symphyseal tritor.

has a well developed aboral area with a robust lateral descending lamina and a low oral region. The latter has a thickness half that of the aboral region in lingual view.

The occlusal surface bears 3 tritoral areas of vascular pleromin arranged linearly: a median tritor with compound cross-section, a smaller outer tritor and a tiny additional outer tritor situated between them. The outer branch of the median tritor is ovoid with a subcircular labial outline and overhangs the labial margin. A box-shaped tritoral bolster with a width of 12 mm corresponds to the outer branch of the median tritor and reaches lingually of the outer branch. The inner branch of the median tritor is just visible along the symphyseal edge of the specimen but is more clearly developed in the lingual cross section of the plate. In this cross section, both inner and outer branches are weakly separated; a whole tritoral body is embossed basally and the basal axis of the median tritor is shifted symphyseally from the axis of the outer branch, visible in occlusal view. The convex form of the basal edge of the median tritor corresponds well with the basal outline of the oral region, visible in lingual view. The median tritor fills most of the oral region except for the distal part of the plate.

In occlusal view, the longitudinal axis of both the outer tritor and the outer branch of the median tritor converge in an apical direction. The location of the outer tritor within the aboral region is not obvious. This tritor is not broad and moderately long, it is well separated laterally from the median tritor and occupies the most distal part of the plate along the labial margin. A tiny additional tritor is located between the anterior edge of the outer tritor and the lateral edge of the outer branch of the median tritor.

Growth lines in the post-occlusal surface are oriented subparallel to the preserved lingual margin. The boundary between the occlusal and post-occlusal surfaces is shifted labially, bypassing lingually all occlusal tritors.

The basal surface shows a large broken lateral descending lamina. This lamina is preserved for the distal third of the plate and shows a maximum visible height of 10 mm; the more symphyseal part of the lamina is poorly preserved and partly (in the center of the basal view) or totally cut mesially. Lingually, the descending lamina shows a well developed basal perforation (Figure 3C, D). A small area of the basal perforation field on the free part of the basal surface is probably present.

Discussion

Restoration of the plate

Based on visible morphological characters, it is possible to restore the missing part of the plate and make some remarks on overall plate morphology (see Figure 2). The plate may have had a broad subtriangular form in occlusal view and a symphyseal margin shorter than both labial and lingual ones based on the trajectories of the labial and lingual margins and the overall shape of the plate.

A tritoral bolster on the chimaeroid mandibular plates, where it exists, is a characteristic posterior element for centrally placed median tritors or labially displaced smaller ones (E.V.P., personal observation). The presence of this bolster on the occlusal surface of the described plate (Figure 2: tbs) may indicate the longitudinal axis of the plate. This conclusion, as well as the rapid narrowing of the aboral part of the plate symphyseally (Figure 2B), suggests that the specimen represents the mandibular plate, with less than 1/10 of the symphyseal part and about 1/3–1/4 of the mesial part having been lost, looking on the occlusal surface.

In lingual view, the curvature of the basal edge of the median tritor's pleromin body, as well as its symphyseal narrowing, indicates the presence of a short inner branch of the median tritor (ibmt). This branch may not reach the outer branch of the median tritor mesially, nor extend to the unpreserved mesial angle of the plate, which must be formed completely by the aboral part of the plate. Also in lingual view, the symphyseal narrowing of the oral part of the plate and its complete occupation by the body of the median tritor excludes the presence of any other tritoral bodies in the symphyseal part of the plate in a cross section, which may result in the absence of any tritors (inner and symphyseal ones) in the reconstructed mesial part of the plate. The outer tritor is, probably, placed on the aboral part of the plate, although the position of the oral-aboral suture is unclear, both occlusally and distally in lingual view.

Based on the disposition of the margins of the plate, the oral-aboral parts and the growth lines, it is possible to suggest that the described plate would have had a subtriangular form in occlusal view and would be characterized by a moderate development of the beak, with no tritors and a less developed superficial inner branch of the median tritor. The reconstructed parts of the plate are shown as broken lines in Figure 2.

Position of the plate in chimaeroid dentition

Despite the incomplete nature of the plate, the holotype MnhnL BM 485 shows greatest similarity to mandibular chimaeroid plates rather than to palatine and vomerine ones because of (1) subtriangular form in occlusal view, (2) the distal location of the outer tritor, (3) the arrangement of all visible tritors along the labial margin of the occlusal surface, (4) the presence of a centrally placed large median tritor, (5) the absence of any trace of a basal pocket on basal surface and (6) the presence of a well developed lateral descending lamina. Additionally, a separate and distally placed outer tritor is typical of the mandibular plates of other Mesozoic chimaeroid taxa and is not confined to callorhinchids only (Stahl, 1999).

All these characters indicate that the described holotype is a mandibular plate and not a palatine nor a vomerine plate. As chimaeroid mandibular plates usually have more taxonomic significance than palatine and vomerine ones (Popov, 2003, etc.), the described plate is sufficient for the diagnosis of a new genus.

Systematic position of *Ottangodus* gen. nov.

Mesozoic chimaeriform holocephalians consist of 3 suborders (Patterson, 1965; Stahl, 1999): (1) Squalorajoidei Patterson, 1965 with a single genus, known from the Early Jurassic (Sinemurian) of England and Italy and the Hettangian of Luxembourg (Delsate *et al.*, 2002), (2) Myriacanthoidei Patterson, 1965 with 8 genera, known from the Late Triassic (Rhaetian) to the Late Jurassic (Tithonian) and (3) Chimaeroidei Patterson, 1965 including 22 genera (Stahl, 1999), authentically recorded from the Early Jurassic (Pliensbachian) to Recent.

Squalorajoid holocephalians can be excluded from comparison because of their characteristic cutting dentition and absence of any record younger than the Early Jurassic (Patterson, 1965; Stahl, 1999). Myriacanthoids are recorded on the basis of several taxa from the Middle to Late Jurassic including several species of *Chimaeropsis* Zittel, 1887 known from the Tithonian of Germany and Belgium as well as several undescribed myriacanthid taxa from the Bajocian of England (Stahl, 1999) and Kimmeridgian of France (Popov *et al.*, 2009). All Jurassic myriacanthids share several morphological characters, some of which could be regarded as plesiomorphic: (1) totally different type of descending lamina forming a high ridge along symphyseal and labial margins and not forming a strip on a basal surface (Figure 4A) (this is probably assumed as a different development of descending lamina in chimaeroid and non-chimaeroid holocephalians: E.V.P., personal observation), (2) absence of tritors on the aboral region of the plates (mandibular plates of callorhinchids have an outer tritor located in the aboral region: Didier *et al.*, 1994; Stahl, 1999; Popov, 2003), (3) occlusal surface with broad coronal vascular tissue organized in pseudotritoral areas by antemortem wear, (4) only coronal organization of pleromin tissue (*vs*. pleromin organization at several levels inside tooth plates in Mesozoic and Cenozoic Chimaeroidei; see Figure 4I) and (5) mainly low oral space in a cross section of the plate compared with the aboral space (see Figure 4A; but excluding *Chimaeropsis* spp., Riess, 1887).

By contrast, *Ottangodus lotharingiae* gen. et sp. nov. shows very strong lateral descending lamina of 'chimaeroid type' (as a broad band on basal surface), superficial but well isolated individual tritors covered lingually by 'compact glossy tissue' (*sensu* Duffin, 1995, 1996) and well developed tritoral bolster over the median tritor (Figure 2). The possible location of the outer tritor on the aboral region of the plate is also typical for primitive chimaeroids (Callorhinchidae) unlike the condition in Myriacanthoidei. On the basis of these characters, *Ottangodus lotharingiae* gen. et sp. nov. cannot be classified as a myriacanthoid chimaeriform.

The presence of a preserved part of a high and well developed lateral descending lamina in MnhnL BM 485 excludes from comparison the Jurassic chimaeroids of the family 'Edaphodontidae' (*sensu* Popov and Beznosov, 2006) such as *Ischyodus* Egerton, 1843 (Figure 4I) and modern Chimaeridae and Rhinochimaeridae, which are characterised by having a more reduced descending lamina (sometimes sectorially reduced as observed in *Elasmodectes* Newton, 1878) as well as a different tritoral pattern including more than 4 or 5 tritors, located in several levels inside the plate.

A cross section of the mandibular plate of *Ischyodus egertoni* (Buckland, 1835) from the Kimmeridge Clay of the UK is shown in figure 4I and represents a typical species of Jurassic 'edaphodontids'. It is obvious that this genus shows a more advanced tritoral pattern with two tritoral levels including a labial one with symphyseal and anterior outer tritors, a strongly but uniformly reduced aboral region (mostly due to the lateral descending lamina), a large space in the oral region of the plate and, additionally, the presence of laminated pleromin in the symphyseal tritor (syt').

With a high lateral descending lamina as well as a restricted number of occlusal tritors *Ottangodus lotharingiae* gen. et sp. nov. can be classified as belonging to the elephant fishes (Callorhinchidae). The Family Callorhinchidae Garman, 1901 *sensu* Popov, 2003 consists of 4–6 genera: *Callorhinchus* Lacépède, 1798 (Late Jurassic–Recent; Figure 4C), *Brachymylus* Woodward, 1892 (Early Jurassic–Late Cretaceous; Figure 4F–H), *Pachymylus* Woodward, 1892 (Middle-Late Jurassic; Figure 4D), *Duffinodus* Popov, 2003 (Callovian, Middle Jurassic; Figure 4E) and, questionably, two early Jurassic genera: *Eomanodon* Ward and Duffin, 1989 (Pliensbachian of England) and *Bathytheristes* Duffin, 1995 (Toarcian of Germany). Mandibular plates are unknown for the last two genera: *Bathytheristes* Duffin, 1995 and *Eomanodon* Ward and Duffin, 1989.

Amongst callorhinchids with known mandibular plates, *Ottangodus lotharingiae* gen. et sp. nov. is most closely related to *Pachymylus leedsi* Woodward, 1892 (Figure 4D) from the Callovian Oxford Clay of England (Woodward, 1892; Stahl, 1999): both taxa have robust plates with tritoral material reduced to two main tritors (median and outer tritors). However, the outer tritor of *P.*

leedsi is usually represented by a series of rounded small pads, the more laterally placed median tritor is more rounded in a cross section, and the oral region of the plate is more developed as well.

Other callorhinchid mandibular plates show differently developed inner tritors (Figure 4E, G, H). While *Brachymylus altidens* Woodward, 1892 from the Callovian Oxford Clay of England shows a poorly developed symphyseal tritor (Figure 4F), a character unique among callorhinchids but typical to 'edaphodontids' (Figure 4I). '*Brachymylus' latus* Duffin, 1996 from the Pliensbachian of Bavaria has no outer tritor unlike the situation in other callorhinchids (Figure 4H). This species also shows some resemblance with *Ottangodus lotharingiae* gen. et sp. nov. by the robustness of the dental plate, the laterally high descending lamina (but decreased in symphyseal direction) and a well-developed median tritor with compound cross section. All the callorhinchid mandibular plates possess a lateral descending lamina which has been reduced to a greater or lesser extent contrarily to the higher descending lamina in *Ottangodus lotharingiae* gen. et sp. nov. These characters, plus the undeveloped oral region and possession of two occlusal tritors, mean that *Ottangodus lotharingiae* gen. et sp. nov. can be regarded as showing a primitive condition within both the Callorhinchidae and the Chimaeroidei as a whole. The unique morphological peculiarities of the Ottange-Rumelange plate allow us to clearly demonstrate that it is different to all described genera of Callorhinchidae and as such, represents a new genus.

Conclusions

(1) An incomplete chimaeroid (Holocephali, Chimaeroidei) mandibular dental plate from the lower Bajocian (*Humphriesianum* Zone) of Ottange-Rumelange, on the Luxembourg-French border is described as a new genus and species of callorhinchid fish *Ottangodus lotharingiae*, gen. et sp. nov.

(2) The described plate shows a set of characters that are primitive for chimaeroids: (A) very high descending lamina, (B) low oral part of the plate, (C) large centrally placed median tritor occupying most of the oral part of the plate and (D) absence of mesio-labial system of the tritors. It therefore represents a basal taxon of the suborder Chimaeroidei.

(3) Within the family Callorhinchidae Garman, 1901, *Ottangodus* gen. nov. is most closely related to the Jurassic callorhinchid species *Pachymylus leedsi* Woodward, 1892 from the Oxford Clay of southern England.

(4) *Ottangodus* gen. nov. is the first recorded member of the Chimaeroidei from the Lorraine Jurassic and the fourth chimaeriform genus known from the Mesozoic of the region.

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Author Contributions

E.V.P. initiated the study and was primarily responsible for the taxonomic aspects, description and discussion as well as producing Figures 2–4. D.D. and R.F. wrote the geological section and R.F. prepared Figure 1. D.D. also contributed to the introduction, description, discussion and references sections. All authors contributed to the writing of the paper.