A CHIMAERID (HOLOCEPHALI, CHIMAERIFORMES) VOMERINE TOOTHPLATE FROM THE UPPER CRETACEOUS OF BELGIUM

by CHRISTOPHER J. DUFFIN

ABSTRACT. The vomerine toothplate of a chimaerid holocephalan (Chondrichthyes) is described from the Emael Chalk (Maastricht Formation, Maastrichtian, Upper Cretaceous) of Eben-Emael, Belgium. A survey and discussion of the vomerine toothplates of Mesozoic chimaeroids confirms the suggestion that the presence of transverse ridges on the post-oral surface of the toothplate is characteristic of chimaerids.

KEY WORDS: Holocephali, Chimaeridae, toothplates, Mesozoic.

THE Holocephali are a group of chondrichthyan fishes ranging in age from Devonian to Recent (Cappetta *et al.* 1993). Cretaceous holocephalans all belong to the Order Chimaeriformes, characterised by the possession of three pairs of toothplates in the dentition, which may be either crushing or sectorial. The lower or mandibular toothplates are opposed by two pairs of toothplates in the upper jaw; the posterior or palatine toothplates are preceded by a pair of anterior or vomerine toothplates.

Vomerine toothplates have received relatively little attention in the literature. This is partly because they are less robust than mandibular or palatine toothplates and, therefore, less commonly preserved. Also, they tend to have fairly conservative development with few taxonomically useful features. The discovery of a well-preserved specimen in Upper Cretaceous deposits gives an opportunity for a brief overview of what is known of vomerine toothplates.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass SUBTERBRANCHIALIA Zangerl, 1981
Superorder HOLOCEPHALI Bonaparte, 1832
Order CHIMAERIFORMES Patterson, 1965
Suborder CHIMAEROIDEI Patterson, 1965
Family CHIMAERIDAE Bonaparte, 1831

Genus and species *incertae sedis*

Text-figure 1A–B

Specimen. IRSNB P.7285 (Institut Royal des Sciences Naturelles de Belgique, Brussels), collected by Mr Guido Bush.

Locality. Marnebel Quarry, Eben-Emael, Belgium; Lava Horizon, Emael Chalk, *Belemnitella mucronata* Zone, Maastricht Formation; Upper Cretaceous, Upper Maastrichtian.

Description. The specimen (Text-fig. 1A–B) is an isolated right upper anterior ('vomerine') toothplate which has been completely freed from the matrix. The descriptive terms used here follow the nomenclature proposed by Patterson (1992) and are summarised in Text-figure 2.

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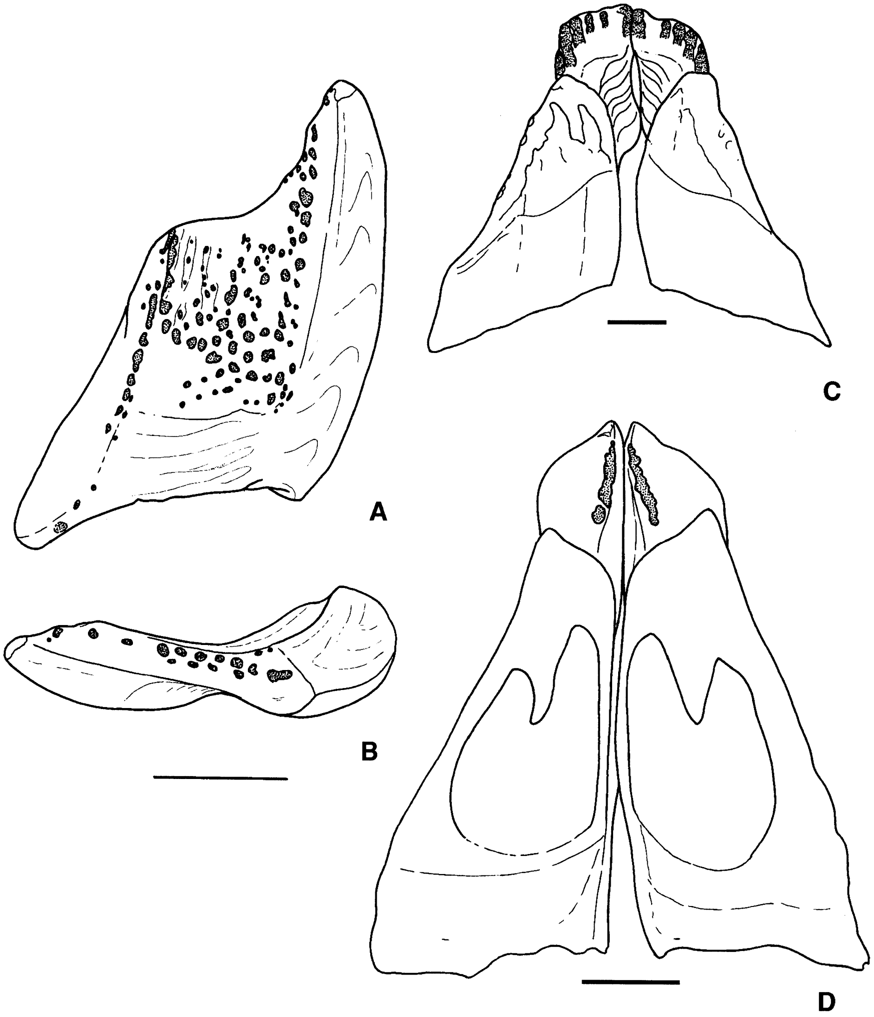
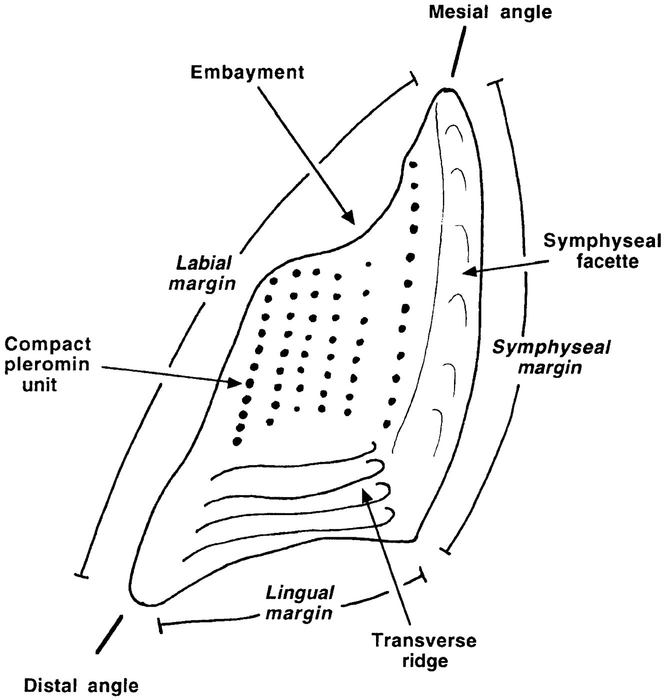


TEXT-FIG. 1. A, IRSNB P. 7285, vomerine toothplate of an undetermined chimaerid holocephalan from the Emael Chalk (Maastricht Formation, Upper Cretaceous, Maastrichtian) of Eben-Emael, Belgium in occlusal view. B, same specimen in lingual view. C, upper dentition of *Chimaera monstrosa* Linnaeus (Recent) in occlusal view. D, upper dentition of *Callorhincus milii* Bory (Recent) in occlusal view. Scale bars represent 1 cm.

Roughly rhombic in outline, the greatest dimension on the toothplate is the diagonal from the mesial angle to the distal angle which is a total of 48 mm (Text-fig. 1A).

The 36-mm-long symphyseal margin is slightly curved toward the mesial angle and marked by a 6-mm-deep symphyseal facette (Text-figs 1A, 2). This would have abutted against a similar facette on the adjacent left vomerine toothplate in life. The mesial angle is sharply pointed. The labial margin has a deep embayment along the mesial third of its length. The lingual margin forms the growth zone of the toothplate; it is 25 mm long and exposes the richly trabecular tissue of the toothplate body, studded with a longitudinal row of at least eight units of compact pleromin, each around 0·7 mm across (Text-fig. 1B).

The basal face of the toothplate was attached firmly to the ethmoid region of the neurocranium in life. The basal surface of the toothplate is flat and relatively featureless; there is no descending lamina. The only noteworthy feature is the somewhat sinusoidal outline of the contact between the vomerine toothplate and the succeeding palatine (upper posterior) toothplate.



TEXT-FIG. 2. Guide to the descriptive terms used in the text.

The occlusal surface is mildly concave anteroposteriorly. The posterior part of the junction between the symphyseal facette and the occlusal surface is accentuated by a slight ridge. A similar ridge marks a change in topography of the surface parallel to the labial margin of the toothplate.

The tritoral tissue of the occlusal surface consists of a series of longitudinal rows of beaded pleromin units, each unit standing proud of the toothplate surface. These constitute the pearlstring dentine of Bargmann (1933), the compact pleromin units of Orvig (1985), or the hypermineralised rods of Didier (1995). There are 12 rough longitudinal rows of hypermineralised rods, which also show a certain amount of lateral alignment. The row closest to the symphyseal margin is composed of 13 rods, the row closest to the labial margin has 11 rods, and a representative central row in the sequence has nine rods. The arrangement into longitudinal rows is not absolutely perfect; occasional isolated rods intervene between well-established rows, disrupting the pattern. Ante-mortem wear of the hypermineralised tissue and its surrounding dentine has produced coalescence of the rods, especially in the two rows adjacent to the labial ridge (Text-fig. 1A).

The posterior part of the toothplate (7 mm wide) has a glossy surface; this is the part of the plate which remained covered with a thin oral epithelium in life. Four transverse ridges cross the tooth plate in this region and presumably represent the surface expression of dormant (i.e. not yet exposed by occlusal action) hypermineralised rods.

DISCUSSION

The tooth plate described above is clearly a vomerine. Chimaeriform, it certainly belongs in the suborder Chimaeroidei rather than in the Myriacanthoidei or the Squalorajoidei. In the myriacanthoids (Late Triassic, Rhaetian – Late Jurassic, Tithonian), the vomerine toothplates (of which there may be one or two pairs) have a triangular outline (e.g. in *Halonodon*; Duffin 1984) and grow in the form of a spiral so that the occlusal surface is strongly convex. The occlusal surface may be covered with a layer of hypermineralised tissue, or possess tritoral areas comprising circular patches of hypermineralised tissue in the form of rods oriented normal to the tooth plate surface and arranged in a series of longitudinal rows (Text-fig. 3A). Up to six rows of tritors are present in such toothplates, with those of the central row being the largest. Tritors in adjacent rows are slightly offset from each other giving a rough secondary arrangement into diagonal rows. This pattern of tritor development and the structure of the hypermineralised tissue contrasts strongly with the condition displayed by the toothplate described from the Maastrichtian of Belgium above.

The distinctive dentition of *Squaloraja* (Squalorajoidea; Sinemurian only) has been described by several authors (Woodward 1891; Dean 1906) and restored by Patterson (1965, fig. 10) (Text-fig. 3B). The vomerine toothplates are small (up to 10 mm long), elongate and have a roughly oval outline. The occlusal surface is convex and there are no localised tritors present. The lamellar strips that cross the toothplate consist of alternating bands of osteonal and interosteonal dentine (Patterson 1965, p. 121) within the hypermineralised tissue, which covers the whole of the toothplate surface.

Extant chimaeroids are currently divided into three families (Didier 1995), each with some fossil genera included; the Callorhynchidae (Callovian – Recent) contains the extant genus *Callorhincus*, the Rhinochimaeridae (Santonian – Recent) incorporates the extant genera *Rhinochimaera*, *Harriotta* and *Neoharriotta*, and the Chimaeridae (Maastrichtian – Recent) embraces *Chimaera* and *Hydrolagus*. Any meaningful discussion of vomerine toothplates must make reference to these families. Table 1 shows the stratigraphic ranges of the genera comprising these three families.

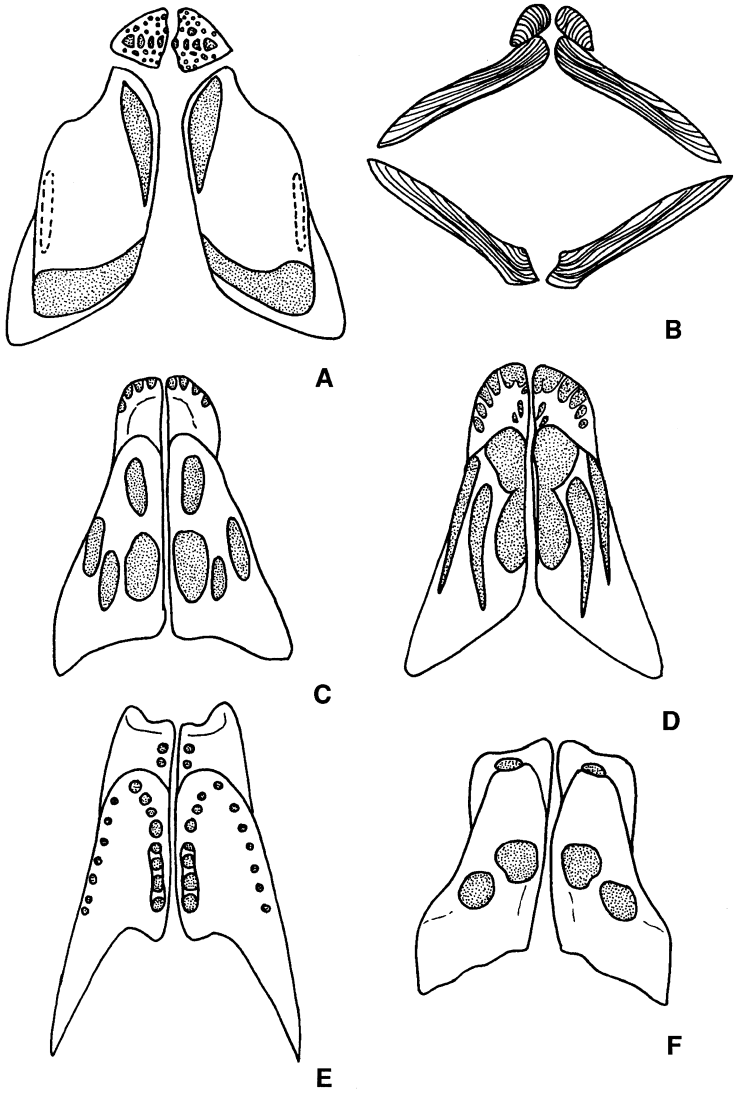
The callorhynchids show the most primitive toothplate conformation (Patterson 1992) with the development of a descending lamina. This is a basal projection from the labial and symphyseal margins of the toothplate, by which it is applied to the margin of the jaw cartilage. According to Didier (1995, p. 51), 'a well developed descending lamina is present on the aboral surface of all tooth plates' in *Callorhincus*, and in the vomerine toothplate in particular, 'there is no obvious hypermineralised tissue exposed on the surface, but histological sections show evidence of a tiny hypermineralised pad in the center of the tooth plate'. The only material available to me was a dentition of *Callorhincus milii*, which has previously been figured by Patterson (1992, fig. 3). Here, the bulk of the toothplate is obscured by the succeeding palatine, but sufficient of the occlusal surface is exposed to permit the identification of an elongate hypermineralised pad formed from the coalescence of a series of hypermineralised rods. The pad is not central in position but forms a longitudinal ridge along the symphyseal margin of the tooth plate (Text-fig. 1D). The condition in extant *Callorhincus* contrasts strongly with that of the Cretaceous vomerine tooth plate, in which there is no descending lamina and the presence of multiple longitudinal rows of hypermineralised rods.

Nessov and Averianov (1996) have described a vomerine toothplate provisionally assigned to *C. borealis* Nessov and Averianov from the Upper Albian of the Belgorod region of Russia. The specimen has three fields of closely spaced hypermineralised rods arranged in rows, and a descending lamina. Similarly, the vomerine toothplate of *Callorhincus* sp. from the Upper Santonian of the Kikino region of Russia possesses a clearly defined descending lamina and a row of six elongate hypermineralised rods near the symphyseal margin (Averianov 1997). The presence of a descending lamina clearly distinguishes these specimens from IRSNB P.2875.

The vomerine toothplate is unknown in a number of fossil callorhynchids (*Leptomylus, Pachymylus*, *Paredaphodon*, *Ptyktoptychion*). In *Brachymylus altidens* Woodward, 1892 (Callovian, England), the vomer shows a strong descending lamina (Ward and McNamara 1977, pl. 66, fig. 5). There is a single ovoid hypermineralised pad located centrally (Text-fig. 3F), in contrast to the Maastrichtian specimen described above. The vomer of *B. bogolubovi* Averianov, 1992 (Middle Volgian, Moscow) possesses five hypermineralised pads on the occlusal surface, and a clearly defined descending lamina (Averianov 1992, fig. 1b).

Ganodus was placed in the Callorhynchidae by Stahl (1999). A large number of toothplates has been collected from the English Bathonian and these are now held in The Natural History Museum (BMNH) and at the Oxford University Museum. A revision of the chimaeroid fauna of the English Bathonian is currently being undertaken by Duffin and Ward. The collection contains a small number of vomerine toothplates which have prominent transverse ridges on the post-oral surface, and small hypermineralised rods on the occlusal surface (Text-fig. 3E).

In *Ischyodus*, the vomerine toothplate has a quadrilateral shape with a slightly arched labial margin (Text-fig. 3C). Most of the vomerine toothplates I have examined from this genus are either abraded or partially obscured by matrix, although a descending lamina is clearly developed in some (e.g. BMNH



TEXT-FIG. 3. Reconstructed upper dentitions from a range of Mesozoic holocephalans. A, *Halonodon warneri* Duffin, 1984 (Myriacanthiformes; Lower Jurassic, Sinemurian, Belgium); B, *Squaloraja polyspondyla* Agassiz, 1836 (Squalorajiformes; Sinemurian, Britain; after Patterson 1965). C, *Ischyodus egertoni* Buckland, 1835 (Chimaeriformes, Family Callorhynchidae; Upper Jurassic, Callovian – Kimmeridgian, Britain). D, *Elasmodus hunteri* Egerton, 1843 (Chimaeriformes, Family Rhinochimaeridae; Eocene, Britain); E, *Ganodus rugulosus* Egerton, 1843 (Chimaeriformes, Family Callorhynchidae; Bathonian, Britain). F, *Brachymylus altidens* Woodward, 1892 (Chimaeriformes, Family Callorhynchidae; Callovian, Britain). Diagrams not to scale.

39101; *I. thurmanni* Pictet and Campiche, 1858, from the Cambridge Greensand, Cambridge, Aptian; Newton 1878, pl. 9, fig. 21). *Edaphodon* has no descending lamina on the vomerine toothplate, but a much reduced descending lamina (in comparison to that of *Ischyodus*) is clearly developed on the mandibular and palatine toothplates. In both *Ischyodus* and *Edaphodon* around five hypermineralised rods erupt along the ventrally-directed occlusal surface.

TABLE 1. Stratigraphic ranges of chimaeroid genera.

		Callorhynchidae												Rhinochimaeridae							Chimaeridae	
		Callorhinchinae							Edaphodontinae													
		Callorhinchus	*Bathytheristes*	*Brachymylus*	*Darbasodus*	*Ischyodus*	*Pachymylus*	*Ptyktoptychion*	*Edaphodon*	*Leptomylus*	*Paredaphodon*	? *Eomanodon*	? *Ganodus*	*Amylodon*	*Elasmodectes*	*Elasmodus*	*Harriotta*	*Lebediodon*	*Psaliodus*	*Stoilodon*	*Belgorodon*	*Chimaera*
Holocene		×															×					×
Pleistocene																						
Pliocene									×													×
Miocene		×				×			×													×
Oligocene														×								×
Eocene		×							×		×			×		×			×			×
Palaeocene		×			×	×										×						
Cretaceous	Maastrichtian					×			×	×						×						
	Campanian					×								×		×						
	Santonian					×											×					
	Coniacian					×																
	Turonian					×			×						×							
	Cenomanian	×				×			×											×	×	
	Albian	×				×		×	×				×					×		×	×	
	Aptian								×													
	Barremian																					
	Hauterivian																					
	Valanginian																					
	Berriasian																					
Jurassic	Tithonian					×																
	Kimmeridgian			×		×									×							
	Oxfordian																					
	Callovian			×		×	×															
	Bathonian					×							×									
	Bajocian					×																
	Aalenian																					
	Toarcian		×																			
	Pliensbachian			×								×										
	Sinemurian																					
	Hettangian																					

One additional specimen of note, BMNH P.47583, is a small incomplete callorhynchid vomerine toothplate from the Gault Clay (Albian) of Small Dole, Sussex. Unlike the Belgian specimen, it has a roughly triangular outline and a strongly developed descending lamina. The occlusal surface is studded with hypermineralised rods arranged in at least eight rows, with the longest row comprising seven rods. There is also a row of three comparatively widely spaced, hypermineralised rods along the symphyseal margin. The post-oral surface carries transverse lines within the glossy tissue covering the body of the toothplate, but has no ridges developed within it.

The superfamily Chimaeroidea, containing the rhinochimaerids and chimaerids, has been partly defined on the basis of the loss of the descending lamina in the vomerine toothplate (Didier 1995, p. 74; her character 91), interpreted as being related to the growth pattern adopted in sectorial rather than crushing dentitions. *Rhinochimaera* itself has no hypermineralised tissue anywhere on any of the strongly sectorial toothplates.

The vomerine toothplates of both *Harriotta* and *Neoharriotta* are incisiform. A series of hypermineralised rods emerges in a row along the ventrally-directed mesial part of the labial margin. Since the two genera are distinguished only on the basis of a separate anal fin in *Neoharriotta*, the dentitions can be considered together.

Neoharriotta has no published fossil record, to the best of my knowledge, but a single species of *Harriotta*, *H. lehmani* Werdelin, 1986, has been described from the Santonian of Sahel Alma in the Lebanon. The specimen preserves the dentition, although the vomerine toothplate has not been described. It requires further study because the generic assignation is by no means certain. Werdelin (1986, p. 395) commented that the palatine toothplate 'resembles the corresponding plate in Recent *Harriotta* . . . . in having a complex pattern of round and elongated tritural columns on its occlusal surface'. The complex of characters described by Werdelin certainly indicates a member of the superfamily Chimaeroidea, but closer comparison with fossil genera such as *Elasmodectes*, *Elasmodus*, *Eomanodon* and *Ganodus* is warranted to clarify its taxonomic position further. Egg cases described from the Upper Jurassic of Canada (Warren 1948) and France (Meunier 1891), as well as the Oligocene of Alaska (Brown 1946) have also been reassigned to *Harriotta* (Stahl 1999).

Other fossil rhinochimaerids include *Amylodon*, *Elasmodectes*, *Elasmodus, Lebediodon* and *Stoilodon*. Nessov and Averianov (1996) have identified nine toothplates from the Belgorod region of Russia as vomerine toothplates of *Lebediodon oskolensis* Nessov and Averianov. These range in age from Late Albian to Cenomanian. The specimens are described as possessing an anterior inner tritor comprising several hypermineralised rods arranged in a longitudinal row at the mesial angle. There is a similar anterior external tritor and a row of up to 33 hypermineralised rods situated along the labial margin of the toothplate. This arrangement is most unusual for a vomerine toothplate and I tend to concur with the suggestion of Popov (pers. comm. 1998) that these specimens are callorhynchid mandibular toothplates. The presence of a descending lamina distinguishes the specimens from the Belgian material.

Stoilodon aenigma Nessov and Averianov (1996) was described from the Upper Albian – Cenomanian of the Belgorod region of Russia on the basis of four specimens. The sectorial toothplates are 'presumably vomerine or, less probably mandibular' (Nessov and Averianov 1996) and lack a descending lamina. The only tritoral material is a group of tiny hypermineralised rods ('point' tritors of Nessov and Averianov, 1996) exposed by post-mortem breakage, providing 'a self-sharpening of the labial edge as wear occurred parallel to the canals simultaneously from the oral and basal sides' (Nessov and Averianov 1996, p. 6). A deep embayment adjacent to the mesial angle is more reminiscent of the conformation of a mandibular tooth plate; *Stoilodon* differs from the Belgian material both in this character and in the lack of hypermineralised rods arranged over the occlusal surface.

Woodward (1891, p. 89) characterised the vomerine toothplates of *Elasmodus* as being 'broad, with several closely-arranged, laminated tritors'. Gurr (1962) subsequently reviewed *E. hunteri* Egerton, 1843 from the Woolwich Bottom Bed (Sparnacian), confusing the palatine and vomerine toothplates. The vomerine ones possess three laminated tritors on the occlusal surface (Text-fig. 3D), although details of the descending lamina are lacking. No transverse ridges are developed on the post-oral surface.

Amongst chimaerids, Didier (1995, p. 52) remarked that the vomerine toothplates of *Hydrolagus* are very similar to those of *Harriotta*, possessing five hypermineralised rods along the mesial part of the labial margin of the toothplate which forms the cutting edge of the incisiform element. The posterior face of the occlusal surface, however, has a series of transverse ridges covered by unworn glossy tissue. This feature is not found in rhinochimaerids, but appears to be a synapomorphy of the Chimaeridae (Didier 1995, p. 75, character 103), also being found in the vomerine toothplates of *Chimaera* (Text-fig. 1C). Other fossil chimaerids for which no vomerine toothplates are known include *Belgorodon* (Nessov and Averianov 1996).

In terms of stratigraphical range, potential generic candidates for the vomerine toothplate described above are *Amylodon* and *Elasmodectes* (for which this element of the dentition is currently unknown), *Lebediodon* and *Stoilodon* (whose vomerine toothplates are probably misinterpreted mandibular toothplates) and *Elasmodus*, whose vomerine toothplate possesses laminated tritors, which are not present on the Belgian specimen.

Amylodon is known from the Eocene and Oligocene of Britain and Belgium, and the Upper Cretaceous of Russia. The type species, *A. delheidi* Storms, 1894 (Rupelian, Belgium), was founded on an abraded mandibular toothplate, although Leriche (1948) later described a palatine toothplate. The mandibular plate has a smooth, blade-like labial margin with a small tritor just behind the beak, and possibly a second, moderate tritor centrally. The palatine plate lacks a middle tritor, but possesses a band-like posterior inner tritor and numerous hypermineralised rods at the mesial angle. *A. eocenica* (Woodward and White 1930) from the Ypresian of England and *A. venablesae* (Casier 1966) from the London Clay (Ypresian) are distinguished from the type species on the form of the posterior inner tritor. *A. emba* Nessov and Averianov, 1996 is based on an isolated palatine toothplate. *A. karamysh* Averianov and Popov, 1995 from the Lower Campanian of Russia is based on an isolated mandibular plate with four median tritors.

Elasmodectes is known from two species, *E. willetti* Newton, 1878 (Turonian, Britain) and *E. secans* Woodward, 1892 (Kimmeridgian, Britain). Both are known from mandibular toothplates only, although Woodward (1912) assigned a partial, articulated specimen to this species (Woodward 1912, pl. 39, fig. 4). Unfortunately, details of the dentition, including the vomerine toothplate, are obscured.

The data from fossil vomerine toothplates can now be used to test Didier's (1995) suggestion that transverse ridges are an apomorphic character of the Chimaeridae, and that the descending lamina is found only in callorhynchids. The last statement is certainly corroborated from the fossil record, with the descending lamina known in vomerine toothplates of *Callorhincus*, *Brachymylus* and *Ischyodus*. *Edaphodon* has no descending lamina on the vomerine toothplate, presumably having lost it secondarily, but it is clearly a callorhynchid on the basis of the weak descending laminae on the mandibular and palatine toothplates. The descending lamina is absent in *Elasmodus, Harriotta*, *Hydrolagus, Lebediodon*, and *Stoilodon* amongst the rhinochimaerids and chimaerids.

Transverse ridges are unknown in the vomerine toothplates of the callorhynchids *Brachymylus, Callorhincus*, *Edaphodon* and *Ischyodus*, and also in those of the rhinochimaerids *Elasmodus, Lebediodon*, and *Stoilodon*. They are present, however, in *Chimaera* and *Hydrolagus*. Vomerine toothplates traditionally referred to *Ganodus* do possess transverse ridges, but are currently under review. Thus, in the current state of knowledge, the presence of transverse ridges appears to be an apomorphy of the Chimaeridae.

In conclusion, the vomerine toothplate from the Belgian Maastrichtian described herein does not belong to any of the Mesozoic and Tertiary chimaeroid genera for which this element of the dentition is known. From the above discussion, the lack of a descending lamina in the vomerine toothplate indicates that the Belgian specimen belongs to the superfamily Chimaeroidea. Although the callorhynchid *Edaphodon* lacks a descending lamina on the vomerine toothplate, the disposition of the tritors and the form of the dental element differs considerably from that in the Belgian specimen. The presence of transverse ridges on the posterior part of the Belgian toothplate indicates an affinity with the chimaerids, although the presence of longitudinal rows of hypermineralised rods is a tritoral arrangement that differs from both of the two extant genera within the family. The only comparable vomerine toothplates known from the fossil record are those that have been ascribed to '*Ganodus*'.

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Averianov (1996) and Averianov (1996) can be found at the following website: http://gause.biology.ualberta.ca/wilson.hp/MF.AVERIANOV%2097Transl.html

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