Description of a new aspidorhynchid fish, *Belonostomus lamarquensis* sp. nov. (Halecostomi, Aspidorhynchiformes), from the continental Upper Cretaceous of Patagonia, Argentina

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Abstract

Some braincases, a predentary, a few vertebrae and scales of a new aspidorhynchid species, *Belonostomus lamarquensis* sp. nov., are described from the Upper Cretaceous (Campanian-Maastrichtian) Allen Formation of Patagonia, Argentina. The new species differs from the other *Belonostomus* species by its flank scales having an anterior smooth region separated by a vertical groove from a posterior region bearing a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin. The dermal bones are ornamented with ridges and tubercles, a rare character in *Belonostomus*. The endocranial bones are completely fused together, except the basisphenoid. Within the *Belonostomus* species, *B. lamarquensis* seems closely related to *B. hooleyi* from the English Lower Cretaceous, which also exhibits dermal bones with ridges and tubercules, and scales morphologically somewhat similar to those of *B. lamarquensis*.

Keywords: Actinopterygii, Aspidorhynchidae, *Belonostomus lamarquensis* sp. nov., neurocrâne, prédentaire, Formation Allen, Cretacé supérieur, Patagonie, Argentine.

Résumé

Quelques neurocrânes, un prédentaire, des vertèbres et des écailles d’une nouvelle espèce d’aspidorhynchidé, *Belonostomus lamarquensis* sp. nov., sont décrits provenant de la Formation Allen d’âge Crétacé supérieur (Campanien-Maastrichtien) en Patagonie, Argentine. La nouvelle espèce diffère des autres espèces de *Belonostomus* par ses écailles des flancs avec une région antérieure lisse séparée par une gouttière verticale d’une région postérieure qui porte de nombreuses crêtes subparallèles pressées les unes contre les autres et qui se terminent au bord postérieur qui est profondément crenelé. Les os dermiques sont ornés de crêtes et de tubercules, un caractère rare chez *Belonostomus*. Les os endocrâniens sont complètement fusionnés entre eux, à l’exception du basisphénôïde. Au sein des espèces de *Belonostomus*, *B. lamarquensis* semble plus particulièrement apparenté avec *B. hooleyi* du Crétacé inférieur d’Angleterre qui montre également des os dermiques avec des crêtes et des tubercules et dont les écailles sont morphologiquement proches de celles de *B. lamarquensis* mais sans être similaires.


Introduction

Aspidorhynchiformes are an order of extinct marine neopterygian fishes characterized by an elongate and low body, a posteriorly displaced dorsal fin opposite to the anal, a long rostrum essentially formed by the dermethmoid (= rostral), and the premaxillae, and a median predentary (DE SAINT-SEINE, 1949: fig. 114; TAVERNE & ROSS, 1973: fig. 2; MAISEY, 1991: fig. p. 175; BRITO, 1997: figs 6, 31, 43, 51; among others). The flanks of their body are covered by very deep and antero-posteriorly narrowed lateral scales whose external surfaces are covered by a thick ganoine layer (WOODWARD, 1908: pl. 30, figs 6, 8; SCHULTZE & STÖHR, 1996: fig. 4; BRITO & MEUNIER, 2000: fig. 1; BARTHOLOMAI, 2004: fig. 10; among others) except in *Aspidorhynchus*, which lacks ganoine on its scales (BRITO & MEUNIER, 2000).

The members of this order have a nearly cosmopolitan geographic distribution with Asia as the only exception (BRITO, 1997: fig. 1), and a biochron extending from the Middle Jurassic to the Late Cretaceous (BRITO, 1997: fig. 2). There is also a mention of an aspidorhynchid predentary in the Early Palaeocene of North America (BRYANT, 1987) but this could be the result of a reworking from Upper Cretaceous layers.

This monophyletic clade contains a single family,
the Aspidorhynchidae, and includes four genera: Aspidorhynchus AGASSIZ, 1833, Belonostomus AGASSIZ, 1834, Vinctifer JORDAN, 1919 and Richmondicthys BARTHOLOMAI, 2004. Current phylogenetic hypotheses place Aspidorhynchus as the most plesiomorphic taxon within the family but there is some disagreement about which genus is the most apomorphic. MAISEY (1991: fig. p. 189) considers Belonostomus as the more specialized genus on the basis of its elongate predentary, whereas TAVERNE (1998) and BRITO (1997, 1999) give that role to Vinctifer because of its advanced caudal characters. Richmondicthys shares with Vinctifer some specialized features of the upper jaw (e.g. the very peculiar shape of the maxilla and the loss of the supramaxilla) but differs from it by the important feature of the shortening of its rostrum (BARTHOLOMAI, 2004).

Aspidorhynchiformes often are considered as evolved halecostomes closely related to Pycnodontiformes, Pachycormiformes, Pholidophoriformes and true teleosts (TAVERNE, 1998: 287; ARRATIA, 2000: figs 20, 21; among others), whereas some researchers place them within teleosts (PATTERSON, 1973: 298; BRITO, 1999b: 262; among others) but this choice essentially depends on the various definitions given by ichthyologists to the taxon Teleostei.

The fossil record of Aspidorhynchiformes in South America is rather rich but restricted to the genera Vinctifer and Belonostomus.

At least three species of Vinctifer are present in the Aptian-Albian deposits of Brazil: Vinctifer comptoni (AGASSIZ, 1841) [= Vinctifer punctatus DA SILVA SANTOS, 1985, cfr. BRITO, 1997: 710], Vinctifer longirostris DA SILVA SANTOS, 1990 and Vinctifer araripensis DA SILVA SANTOS, 1994. Scales of a Vinctifer sp. are known from the Barremian of Brazil (BRITO et al., 1994). Remains of Vinctifer sp. are reported also from the Aptian-Albian of Venezuela (MOODY & MAISEY, 1994) and from the Aptian of Colombia (SCHULTZE & STÖHR, 1996). Finally, a partial braincase of Vinctifer sp. is briefly mentioned and poorly illustrated from the Campanian of Patagonia (BRITO, 1997: 714, fig. 29), but BARTHOLOMAI (2004: 535) pointed out that this material does not show enough characters in order to refer it to a peculiar aspidorhynchid genus.

It is to be noted that what we herein re-identify as Vinctifer sp. (called Belonostomus in TAVERNE, 1969) is also known from the Aptian-Albian Cocobeach Formation of Equatorial Guinea, an African geological formation, which at that time, when South America and Africa began to separate from each other, was geographically close to those of Brazil.

Regarding Belonostomus, there are several records of isolated jaw bones in some Maastrichtian fossiliferous localities from Patagonia (Argentina) and Chile (CASAMIQUELA, 1992; BRITO & SUAREZ, 2003). All these specimens were referred to the North American Late Cretaceous species Belonostomus longirostris LAMBE, 1902, based on the morphology of those bones. Some fragments of a Belonostomus sp. have been described from the Kimmeridgian of Argentina (LEANZA & ZEISS, 1990) but BRITO (1997: 745) referred them to Vinctifer for paleobiogeographic reasons. “Belonostomus” carinatus MAWSON & WOODWARD, 1907 from the Barremian of Brazil has been shown by BRITO (1997: 745-746) to be an undetermined holostean and not an aspidorhynchid.

Aspidorhynchus is not present in South America but one species, Aspidorhynchus arawaki BRITO, 1997, is recorded in the Oxfordian of Cuba (BRITO, 1999a). Richmondicthys, the closest allied genus of Vinctifer, is confined to the Albian of Australia (BARTHOLOMAI, 2004).

The aim of the present paper is to describe the newly discovered material of a new Belonostomus species from the continental Campanian-Maastrichtian beds of the Allen Formation, in northern Patagonia, Argentina. We have re-examined the specimen MACN RN 1078 figured by BRITO (1997: fig. 29) and considered by him as a Vinctifer sp. Its proportions, its large size, the disposition of the endocranial foramina, as well as the extensive fusion of endocranial bones, are in all points identical to our own samples. Therefore, we reassign that specimen to the new Patagonian species described below.

Geographic and stratigraphic position (Fig. 1)

The specimens here described were collected in the fossiliferous locality of Cerro Tortuga at Santa Rosa Basin (see NOVAS et al., 2008), Río Negro province, Patagonia, Argentina. This locality is located at 39°26′50″S, 67°19′20″W. It is characterized by the presence of extensive outcrops belonging to the Campanian-Maastrichtian (Upper Cretaceous) Allen Formation (APESTEGUIA, 2002; LEANZA et al., 2004). The deposits of the Allen Formation comprise siltstones and sandstones showing evidence of a lacustrine and fluvial environment (CASADIO, 1994).

Cerro Tortuga yielded a large amount of fossil vertebrates, including dryolestoid and gondwanatherian mammals, basal birds, theropods, saurischians, and ornithischian dinosaurs, as well as leptodactylid and pipid frogs, chelid turtles, sphenodontid lizards,
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madtsoid snakes, and a wide variety of fresh-water fishes (BRITO, 1997; CORIA, 2001; CLARKE & CHIAPPE, 2001; HOPE, 2002; MARTINELLI & FORASIEPI, 2004; APESTEGUIA & ROUGIER, 2007; NOVAS et al., 2008; ROUGIER et al., 2009; BOGAN et al., 2010), and freshwater mollusks (HUGO & LEANZA, 2001).

Systematic paleontology

Sub-class Actinopterygii KLEIN, 1885
Division Halecostomi REGAN, 1923
Order Aspidorhynchiformes BLEEKER, 1859
Family Aspidorhynchidae
NICHOLSON & LYDEKKER, 1859
Genus Belonostomus AGASSIZ, 1834

Type species: Belonostomus tenuirostris (AGASSIZ, 1833)

Belonostomus lamarquensis sp. nov.
Figs 2-13

Derivatio nominis
From the city of Lamarque, Argentina.

Holotype
MML 454: an incomplete neurocranium.

Paratypes
MML 456: an incomplete neurocranium; MML 455: an incomplete skull roof; MML 450: an incomplete predentary; MML 464: an incomplete basioccipital bone; MML 524-69: vertebrae; MML 577: some articulated scales associated with a posttemporal; MML 578: a complete basioccipital with associated abdominal vertebrae; MML 841: a basioccipital region of a neurocranium; MML 844: more than one hundred scales; MACN RN 1078: an incomplete neurocranium.

Diagnosis
A large sized Belonostomus differing from the other species of the genus by having its flank scales divided in an anterior region with a smooth surface and a posterior region bearing a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin, the two regions being separated by a conspicuous vertical groove. Long predentary bearing large teeth in its median gutter and small teeth on its lateral margins. Ganoid layer of the dermal bones ornamented with ridges and tubercles. Frontal and parietal fused together. Deep irregular interdigitations between the two fronto-parietals. Dermopterotic and supratemporal fused together. Endocranial bones of the braincase completely fused, except the basisphenoid.


Description
The skull (Figs 2-10)

MML 450 is a fragment of an elongated, narrow and relatively large predentary. The piece measures 1.7 cm in length. Its outer face lacks the strong ganoine cover that is present in other Belonostomus species (see, e.g. TAVERNE & ROSS, 1973: fig. 2) but it is, however, feebly ornamented by some longitudinal ridges. There is a well-marked groove along the middle of its oral face. A series of four large conical teeth are preserved in that median gutter. The apexes of those teeth are missing and the wide pulpar cavity is visible. As usual in Belonostomus, each lateral margin of the bone bears a row of smaller teeth (FELIX, 1891: pl. 28, fig. 16; WOODWARD, 1908: pl. 30, figs 3, 4; BARBACK, 1968: fig. 1C, D; WHETSTONE, 1978: fig. 8; BRYANT, 1987: fig. 1) of which only the bases are preserved. Ventrally, the bone has a weak median keel, laterally delimited by shallow grooves. The suture for the articulation with the dentaries is narrow and shaped as an inverted “V”.

Fig. 2 - Belonostomus lamarquensis sp. nov. Fragment of the predentary MML 450 in lateral (above) and upper (below) views.

All five neurocrania have lost their rostrum and their orbital portion. Only the region between the sphenotic and occipital levels is preserved; i.e., the braincase itself.

The dermal bones of the skull roof are covered by a thick ganoine layer and have a conspicuous ornamentation composed by tubercles and well-developed ridges.

The frontal and the parietal of each side are fused in a compound fronto-parietal which covers with its antimere most of the skull roof. Each fronto-parietal is strongly asymmetrical and has a complex median suture, which is displaced to the right half of the skull. This median suture is very sinuous and has irregular interdigitations. Laterally, the fronto-parietals end in a right lateral margin, like a step. The dermopterotic and the extrascapular of each side also are fused in a dermopterotic-extrascapular. These bones are poorly preserved in all the samples. They are asymmetrical, and the dermopterotic part of the compound bone is anteriorly projected.

In ventral and posterior view, all the braincases exhibit a notable fusion among the endocranial bones, which generally prevents distinguishing sutures between these bones. This condition was previously noted by BRITO (1997: 714) and BARTHOLOMAI (2004: 535) for the paratype specimen MACN RN 1078. However, on the right side of the skull of the holotype,
traces of the sutures between the ascendant process of the parasphenoid and the autosphenotic, between the prootic and the opisthotic, and between the intercalar and the exoccipital are still discernible.

The orbitosphenoid is missing. The meningost of the basisphenoid is preserved on the braincase MACN RN 1078 and is not fused to the other endocranial bones of the braincase. The two pterosphenoids comprise the boundaries of a very large median opening for the two optical nerves (II), and more dorsally of a smaller median opening for the two olfactive nerves (I). Each pterosphenoid is pierced by at least three foramens. The foramen for the trochlear nerve (IV) is located on the dorsal robust wing of the bone. More ventrally, there is the trigemino-facial chamber with a broad foramen for the exit of the ramus profundus (V'), the trigeminal nerve (V), the rami ophthalmicus and buccalis of the facial nerve (VII), the jugular vein and the orbital artery. Near this opening, but more medially, there is another smaller foramen for the common oculomotor nerve (III).
The autosphenotics form a large protuberance on each side of the skull. The autopterotics seem to be fused with the dermopterotics. The prootics and opisthotics are ventrally grooved to form a deep and wide gutter, constituting the jugular depression together with that for the articulation with the hyomandibula. On its ventral surface, the prootic has two foramens, one anteriorly located for the truncus hyoideomandibularis of the facial nerve (VII), and one posteriorly, near the region of contact with the opisthotic, parasphenoid and basioccipital, for the exit of the glossopharyngeal nerve (IX). The opisthotics are large bones connected anteriorly with the prootics and posteriorly with the intercalars and exoccipitals but the sutures are generally not clearly visible. In all our samples, the posterior processes of the intercalars are broken away.

The parasphenoid is toothless and posteriorly fused to the basioccipital. The rear extremity of the parasphenoid is constricted at the level of a subvertical groove on each side of the basioccipital. Towards its anterior end, the bone becomes wider and forms a bulbous structure of ojival contour until the level of the paired ascending processes of the parasphenoid. These ascending processes are robust, wide, laterally oriented and strongly bulging. They are continuous with the pterosphenotics and autosphenotics, all these bones being fused, constituting a single structure. The two small foramens for the internal carotid arteries are located at the basis of the ascending processes. A little forward on the middle of the parasphenoid, there is another pair of small and closely spaced foramens for the efferent pseudobranchial arteries. This situation is similar to that present in Vinctifer (Brito, 1992: fig. 2), whereas in Richmondichthys, these foramens are located on the ascending processes themselves, distant from the midline (Bartolomai, 2004: fig. 7C). The parasphenoid of the holotype is crushed in that region and the foramens for the efferent pseudobranchial arteries are not preserved. On both sides, at the region between the ascending process of the parasphenoid and the prootic and just before the foramen for the truncus hyoideomandibularis of the facial nerve (VII), there are two other foramens, one medially located through which the orbital artery enters in the trigemino-facial chamber, and one just above, at the anterior end of the jugular gutter on the prootic, allowing the penetration of the jugular vein in the trigemino-facial chamber.
A new aspidorhynchid fish from the Upper Cretaceous of Argentina (see Brito, 1997), but is absent or reduced in Richmondichthys. Anteriorly and dorsally to the lateral basioccipital process, there is a strong osseous bump, anteriorly delimited by a subvertical deep groove. At the basis of this groove, the basioccipital is on each side pierced by a small foramen for the occipital artery, a condition not mentioned in other aspidorhynchids but known in many actinopterygians. The sutures between the exoccipitals and the basioccipital are not clearly visible. However, it seems that the large foramen for the vagus nerve (X) on each side of the skull is open at the edges between these bones and just above and anterior to the subvertical groove. Immediately posterior to the vagus foramen, there is a smaller additional foramen for an occipito-spinal nerve (XI). Such a structure is also seen in Richmondichthys (Bartolomai, 2004; fig. 6B). On its internal surface, the anterior region of the basioccipital has wide articular surfaces for the parasphenoid. The paratype MML 456 has lost its basioccipital and the posterior end of the myodome cavity is visible behind the parasphenoid and just below the foramen magnum, indicating that the myodome enters in the basioccipital region.

The supraoccipital is evident as a well-developed median bony knob on the rear-face of the braincase. The sutures between the supraoccipital, the epiotics (= epicellulars), the autopterotics, the intercalars and the exoccipitals are not clearly visible. However, on each side of the supraoccipital, in the region of the epiotic, autopterotic, intercalar and exoccipital, there is a large but not deep depression, the temporal (= posttemporal) fossa.

The girdles (Fig. 12) An important part of a large right posttemporal is preserved on sample MML 577. The bone is as deep as long, and much broader ventrally than dorsally. Its surface is strongly ornamented with ridges and tubercles. The anterior and ventral borders of the bone are straight and the posterior border convex.

The axial skeleton (Fig. 11) The vertebrae are amphicoelous and holospondylous, with a wide opening in their centre for the passage of the notochord. Their ventral surface is nearly flat, but has a median longitudinal ridge, which is low and round. The neural arches are fused to the centra and contain a closed neural canal. Above this canal, there are two narrow and elongate neural spines. The neural...
arcs bear a pair of small pointed prezygapophyses. The haemapophyses (= parapophyses) are located near the ventral margin of the vertebral body and are fused with it. They are laminar, short and wide.

*The squamation* (Fig. 12)
In the same fossiliferous deposits, there are large numbers of lateral scales that are clearly referable to the Aspidorhynchidae. Among the materials, there are a row of associated scales with a fragment of strongly ornamented bone, probably a posttemporal or a fragment of opercle. The ornamentation of this bony fragment is in all points similar to that of the dermal bones of the four braincases, allowing us to refer all these scales to *B. lamarquensis* sp. nov.

The lateral scales are dorsoventrally elongate and subrectangular in shape. They are covered by a thick ganoine layer. On the best-preserved scales, there is a posterior region with a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin. In this way, the scale has a pectinate general shape. The posterior region with the ridges is separated by one conspicuous vertical groove from a deep but narrow anterior region with a smooth surface. On the internal surface, there is a poorly defined concave-convex articulation, representing the last trace of the actinopterygian peg and socket system and characteristic of aspidorhynchid scales.

**Discussion**

The presence of a long predentary undoubtedly attests that the Patagonian species belongs to the genus *Belonostomus* because the three other aspidorhynchid genera possess short predentaries (Fig. 13).

Its very peculiar scales are another argument to include the species from Argentina in the genus *Belonostomus*, because deepened lateral scales with a vertical groove between a smooth anterior zone and a posterior region with ridges ending in a crenulated border also exist in another species of this genus, *Belonostomus hooley* WOODWARD, 1916 from the Lower Cretaceous of England and the Isle of Wight (WOODWARD, 1916-1919: 100-101, pl. 21, figs 1, 3). However, the ridges in the English species are less numerous and the crenulation more coarse. Such flank scales are unknown in other aspidorhynchid species.

The ornamental condition of the skull roof in *B. lamarquensis*, with marked tubercles and broad ridges, resembles more that in *Aspidorhynchus* (WOODWARD, 1895: 419, 423, 426, 427, 1916-19: 97, fig. 33), *Vinctifer* (BRITO, 1997: 698) and *Richmondichthys* (BARTHOLOMAI, 2004: 529) than that of most *Belonostomus* species, in which the cranial roof is nearly smooth or ornamented with long and thin ridges (TAVERNE & ROSS, 1973: fig. 2). But there is one exception because the English *B. hooley* exhibits dermal skull bones “very coarsely ornamented with irregular rounded ridges and low elongated tubercles” (WOODWARD, 1916-1919: 100).

The deep interdigitations between the two frontoparietals are more like the situation in *Vinctifer* (MAISEY, 1991: fig. A on p. 175; BRITO, 1997: fig. 9) and *Richmondichthys* (BARTHOLOMAI, 2004: fig. 7A) than that in *Belonostomus* or *Aspidorhynchus*, in which the interdigitations are less pronounced (WOODWARD, 1916-1919: fig. 33).

*B. lamarquensis* sp. nov. has an extensive fusion of endocranial bones, as is normal in the genus *Belonostomus* (TAVERNE, 1981: fig. 5; BRITO, 1997: fig. 49). In *Vinctifer*, young specimens have clearly
visible sutures between the endocranial bones (BRITO, 1992: fig. 2) while those bones are fused in older specimens (MAISEY, 1991: fig. p. 178). *Aspidorhynchus* and *Richmondichthys* retain the unfused condition (WOODWARD, 1916-1919: fig. 33; BARTHOLOMAI, 2004: fig. 7B, C).

When referring specimen MACN RN 1078 to the genus *Vinctifer*, BRITO (1997) has expanded the biochron of the genus from the Early Cretaceous to the uppermost Cretaceous, indicating that it was not an exclusively Aptian-Albian genus as previously had been thought, and that the *Vinctifer* biozone, characteristic of such a time span, may be rejected. Our own observations do not corroborate BRITO’s (1997) conclusions because the Late Cretaceous Patagonian aspidorhynchid is not a *Vinctifer* but a *Belonostomus*.

*B. lamarquensis* sp. nov. constitutes the southernmost species of the genus, and, on the basis of the available information, may be considered as a freshwater species, based on the evidence yielded by the geology of the fossiliferous outcrops. In the strata belonging to the Allen Formation, the new species appears to be abundantly represented by scales, vertebrae and isolated skull fragments, suggesting that it was a rather common inhabitant of this paleoenviroment during the Campanian-Maastrichtian interval.

The Patagonian Upper Cretaceous fragments of aspidorhynchid fish (CASAMIQUELA, 1992; BRITO & SUÁREZ, 2003) attributed until now to *Belonostomus longirostris*, a species known from the Cenomanian of North America, very probably belong to *B. lamarquensis*.

Conclusions

The highly specialized flank scales prove that *B. lamarquensis* sp. nov. deserves its pecuilar specific status. Those scales, the ridges and tubercles on the dermal bones of the skull and the very large size of the fish denote a closer relationship of *B. lamarquensis* with *B. hooleyi* than with the other species of *Belonostomus*.

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List of institutional abbreviations

MML: Museo Municipal de Lamarque, Rio Negro province, Argentina.

List of abbreviations used in figures

APTE: autopterotic
ASPH: autosphenotic
BO: basioccipital
BSPH: basisphenoid
DPTE: dermopterotic
EPI: epiotic (= epicoccipital)
EXO: exoccipital
FR: frontal
HAEMAP: haemapophysis (= parapophysis)
IC: intercalary
NEUR: neural arch
NEUREP: neural spine
OPIS: opisthotic
PA: parietal
PN: predentary
PSE: prootic
PS: parasphenoid
PSPH: pleuropshenoid (= pterosphenoid)
SOC: supraoccipital
ST: supratemporal (= extrascapular)
V: vertebral centrum
VI: first vertebra
f. I: foramen of the two olfactive nerves (I)
f. II: foramen of the two optic nerves (II)
f. III: foramen of the common oculomotor nerve (III)
f. IV: foramen of the trochlear nerve (IV)
f. V° + V + VII o. a. + j. v.: foramen for the anterior exit from the trigemino-facial chamber of the *ramus profundus* (V°), the trigeminal nerve (V), the *rami ophthalmicus* and *buccalis* of the facial nerve (VII), the orbital artery and the jugular vein
f. IX: foramen of the glossopharyngeal nerve (IX)
f. X: foramen of the vagal nerve (X)
f. XI: foramen of the occipito-spinal nerve (XI)
f. e. p. a.: foramen for the effenter pseudobranchial artery
f. hyom.: fossa for the articulation with the hyomandibula
f. j. v.: foramen for the posterior entering of the jugular vein in the trigemino-facial chamber
f. o. a.: foramen for the posterior entering of the orbital artery in the trigemino-facial chamber
References


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