AMEGHINIANA - 2012 - Tomo 49 (1): xxx - xxx ISSN 0002-7014

THREE DIMENSIONAL ANGEL SHARK JAW ELEMENTS (ELASMOBRANCHII, SQUATINIDAE) FROM THE MIOCENE OF SOUTHERN ARGENTINA

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Key words. Squatina. Neogene. Patagonia. Tessellated cartilage. Taphonomy

Palabras claves. Squatina. Neógeno. Patagonia. Cartílago teselado. Tafonomía

Surveying the basal beds of the middle–late Miocene Puerto Madryn Formation near the city of Puerto Madryn, northeastern Chubut province, Argentina (Fig. 1), one of us (MC) collected the proximal half of a palatoquadrate (upper jaw) and the Meckel's cartilage (lower jaw) of an angel shark (*Squatina* Dumeril, 1806).

Fossil chondrichthyans are usually represented by isolated teeth, spines, and scales whereas endoskeletal remains are extremely rare due to their low preservation potential (Cappetta, 1987). The most abundant cartilage preserved is the vertebral centrae.

The endoskeleton of elasmobranch fishes (sharks, rays, and relatives) is composed by cartilage instead of bone as in other vertebrates. This cartilage may be mineralized to varying degrees with crystals of hydroxyapatite, giving stiffness to the skeletal system. There are two types of skeletal cartilage in sharks: the vertebral cartilage (present only in vertebrae) and the tessellated cartilage (present in the rest of the skeleton) (Fig.2.1).

The tessellated cartilage consists of a mosaic of hexagonal tiles called tesserae (Fig. 2.2–5), joined together by intertesseral collagen fibers. The tesserae are lying just beneath the fibrous perichondrium and overlaying a core of unmineralized extracellular matrix containing chondrocytes (Kemp and Westrin, 1979; Dean and Summers, 2006). Three-dimensionally preserved endoskeletal cartilages are uncommon in the fossil record because tessellated tissues tend to collapse after the decay of the unmineralized inner core and other soft tissues. Tessellated cartilages are often found as two dimensional elements, patches of tesserae or isolated tesserae. In southern South America, endoskeletal elements other than vertebrae are restricted to the skeleton of a primitive batomorph from the Jurassic of Patagonia (Cione, 1999).

Squatina is a neoselachian genus known since the Cretaceous (Welton and Farish, 1993). In southern South America, teeth of *Squatina* have been reported from the Upper Cretaceous, probable the Paleocene and Miocene of Chile (Gutstein *et al.,* 2008; Muñoz-Ramírez *et al.,* 2008), and the Miocene of Argentina (Ameghino, 1906; Cione, 1988; Cione *et al.,* 2000, 2005). In the Puerto Madryn Formation, teeth of *Squatina* were previously preserved as stomach content of the pinniped *Kawas benegasorum* Cozzuol, 2001. In this note, the jaws of *Squatina* sp found in the Puerto Madryn Formation are described and the taphonomic context is discussed.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE

The jaws of *Squatina* sp comes from the basal strata of the Puerto Madryn Formation, cropping out at cliffs located to the west of the city of Puerto Madryn (65°06'W; 42°46'S) (Fig. 1.1). The Puerto Madryn Formation (*"Entrerriense"* plus *"Rionegrense marino"* of Feruglio, 1949) corresponds to the late part of the extensive marine encroachment that lasted from the late Oligocene until the late Miocene ("Mid Tertiary Transgressive Onlap Sequence" of Williams and Hubbard, 1984) paralleling the early Neogene trend of the global eustatic rise (Uliana and Biddle, 1988; Del Río, 1991; Del Río *et al.,* 2001). The Puerto Madryn Formation overlies the Gaiman Formation (early Miocene) in the Península Valdés and lower Chubut river area. The large areal extent of

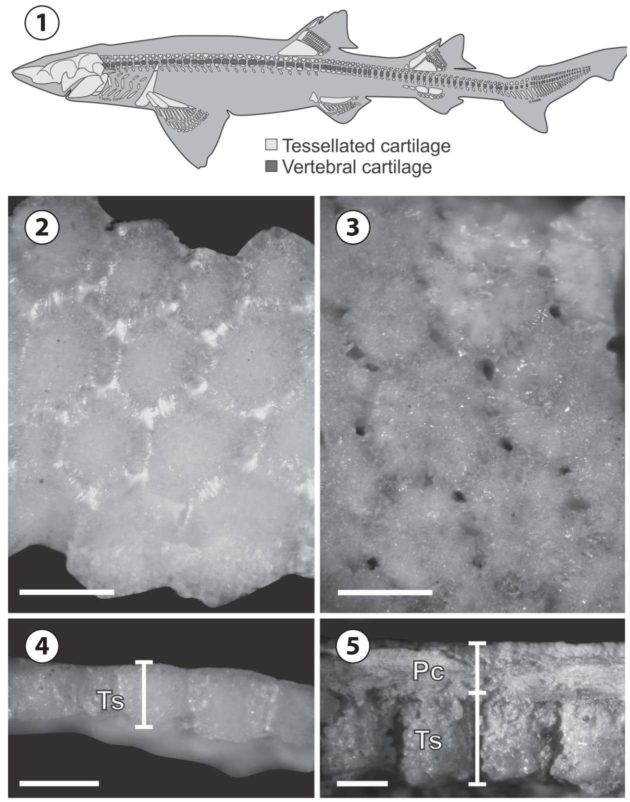

Figure 2. 1, Schematic draw showing the distribution of the tessellated cartilage and the vertebral cartilage in elasmobranchs (modified after Dean and Summers, 2006)/ *dibujo esquemático mostrando la distribución del cartílago teselado y cartílago vertebral en elasmobranquios (modificado de Dean and Summers, 2006);* **2, 4,** Tessellated cartilage of a extant specimen of ***Squatina***. Internal surface and cross section view respectively. Scale bar= 500 µm/ *cartilago teselado de un ejemplar actual de* **Squatina**. *Superficie interna y vista en sección transversal respectivamente. Escala= 500 µm;* **3, 5,** Tessellated cartilage of the fossil palatoquadrate MPEF-PV 3804. Internal surface and cross section view respectively. Scale bar= 500 µm/ *cartilago teselado del palatocuadrado fósil MPEF-PV 3804. Superficie interna y vista en sección transversal respectivamente. Escala= 500 µm;* **Pc,** perichondrium/ *pericond*

Miocene marine deposits reveals that the mean freeboard of the plate interior was low (Uliana and Biddle, 1988).

The Puerto Madryn Formation consists of a sequence of coquinas, cross-bedded sandstones, shales with heterolithic lamination and massive shales totally bioturbated or laminated (Haller, 1981; Del Río, 2000). According to Scasso and Del Río (1987), the sequence belongs to a transgressive-regressive cycle within an overall regressive sequence. These sediments were deposited on a shallow shelf with storm influence, evolving upwards into a tide-dominated estuarine environment.

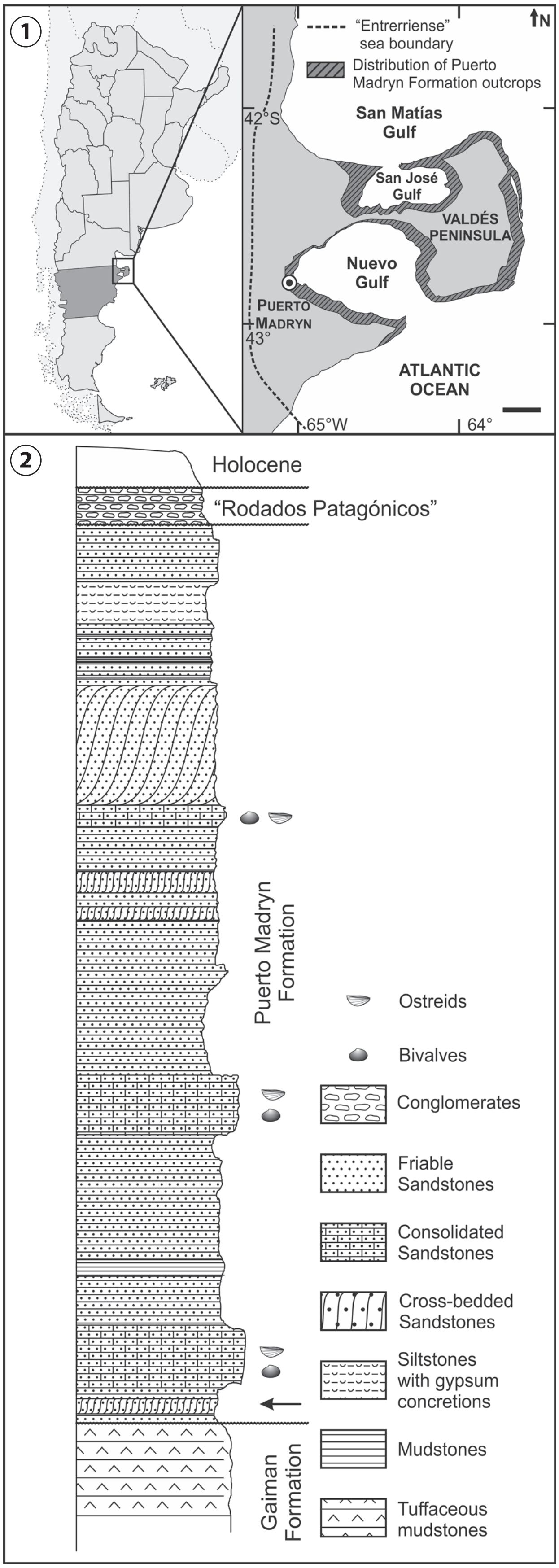

Figure 1. 1, Locality map of Puerto Madryn (modified after Cozzuol, 2001)/ *mapa de la localidad de Puerto Madryn (modificado de Cozzuol, 2001);* **2,** Stratigraphic section exposed at the cliff near the local racetrack (modified after Haller, 1981). The arrow points to the fossil bearing level/ *perfil expuesto en cercanías del autódromo local (modificado de Haller, 1981). La flecha señala el nivel donde provienen los fósiles.*

The material described herein was obtained in the middle section of the cliffs located at the west of Puerto Madryn city, near the local racetrack. The fossil bearing beds correspond to accumulations of the Transgressive Phase of Del Río *et al.* (2001) located at the base of the Puerto Madryn Formation (Fig. 1.2).

The age of the Puerto Madryn Formation has been widely discussed. In recent years, it has been referred to the middle Miocene (biostratigraphic evidence; Del Río 1988) and more recently to the early late Miocene (strontium datations; Del Río *et al.,* 2001; Scasso *et al.,* 2001). However, according to cetacean evidence, the deposition appears to have started during the middle Miocene up to the Tortonian (Cione *et al.,* 2005). We agree with this later hypothesis.

SYSTEMATIC PALEONTOLOGY

Subclass ELASMOBRANCHII Bonaparte, 1838

Order SQUATINIFORMES Buen, 1926

Family SQUATINIDAE Bonaparte, 1838

Genus ***Squatina*** Dumeril, 1806

Type species. *Squalus squatina* Linnaeus, 1758.

Distribution. Recent species lives in temperate European and North African deep waters, to at least 150 m (Compagno 1984).

Squatina sp.

Figure 3.1–3.2

Material. MPEF-PV 3804, right palatoquadrate (upper jaw) and MPEF-PV 3805, right Meckel's cartilage (lower jaw), corresponding to a single specimen.

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Description. The material consists of a partial right palatoquadrate and Meckel's cartilage, both three-dimensionally preserved. The symphysial area is missing. The palatoquadrate is elongated and has a shallow dental groove on the mesial surface. The most proximal portion is developed into an articular process of the palatoquadrate, which articulates with the concave articular fossa of the Meckel's cartilage. Immediately mesial to the articular process, there is the shallow quadrate concavity, which in turn receives the mandibular knob. The quadrate process is a small and dorsally-directed triangular process located in the proximal one-third of the dorsal surface (Carvalho *et al.*, 2008; Fig. 3.1). The Meckel's cartilage has a sharp dental groove on the mesial surface. A well-developed mandibular knob is preserved on the articular area, but the mandibular articular fossa is worn. The palatoquadrate and the Meckel´s cartilage have well-preserved tessellated tissue. In cross section, individual tesserae can be clearly observed, and overlaying them, there is a thin layer that appears to be the calcified perichondrium (Fig. 4). Tesserae are hexagonal in shape and they are higher than wide, ranging from 600–800 µm wide and 800–1000 µm high (Fig. 2.3, 2.5). Both cartilages have an inner cavity completely filled by fine-grained sand. No associated teeth were found.

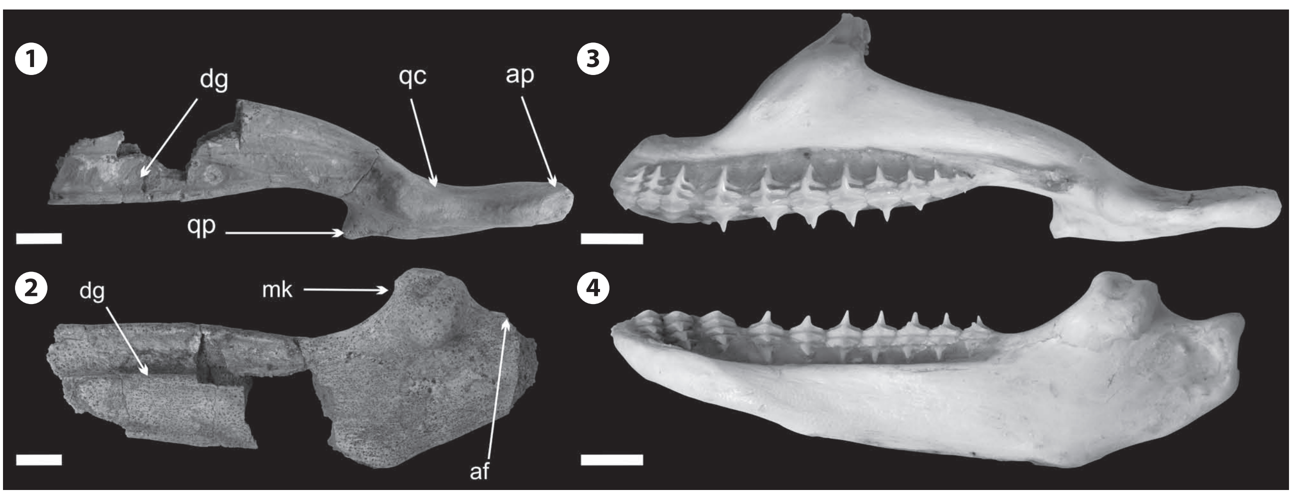

Figure 3. ***Squatina*** jaws in lingual view/ *mandíbulas de* **Squatina** *en vista lingual.* **1,** MPEF-PV 3804 fossil right palatoquadrate (upper jaw)/ *MPEF-PV 3804 palatocuadrado fósil derecho (mandíbula superior);* **2,** MPEF-PV 3805 fossil right Meckel's cartilage (lower jaw)/ *MPEF-PV 3805 Cartílago de Meckel fósil derecho (mandibular inferior);* **3**–**4,** extant *Squatina* palatoquadrate and Meckel's cartilage respectively. Scale bars= 10 mm/ *palatocuadrado y cartílago de Meckel respectivamente de un ejemplar actual de* Squatina*. Escala= 10 mm.* **af,** articular fossa/ *foseta articular*; **ap,** articular process/ *proceso articular*; **dg,** dental groove/ *surco dental*; **mk,** mandibular knob/ *perilla mandibular*; **qc,** quadrate concavity/ *concavidad cuadrada*; **qp,** quadrate process/ *proceso cuadrado.*

DISCUSSION

The material agree with the jaws of species of *Squatina* and differs from other neoselachians in the general shape, the size and proportions of the dental groove, the position and shape of the mandibular knob, the elongate proximal section of the Meckel`s cartilage (the articular process and quadrate concavity are widely separated), and the small size and peculiar shape of the quadrate process (which has no direct suspensory function and is a derived feature of angel sharks; see Compagno, 1977; Carvalho *et al*., 2008) (Fig. 3.3–4).

As tessellated cartilage is very labile, its preservation requires scarce transport, lack of scavengers, and rapid burial (Martin, 1999). Schäfer (1972) studied under experimental conditions the modes of disintegration of fish carcasses and the time it involves. In the case of chondrichthyans, soft tissues were completely disintegrated 20 days after death and only the jaws, teeth, remains of fin rays, and some placoid scales left over. Moreover, this rate of decay steeply increases in well-oxygenated waters. The fossil bearing stratum corresponds to the transgressive phase and was deposited in an environment above the storm-wave base, swept by strong tidal currents (Scasso and Del Río, 1987; Del Río *et al.,* 2001). This kind of environment is characterized by a high level of oxygenation and aerobic degradation, which has an important role in soft tissue decay. Aerobic degradation often entails the body to refloat by gas developed in the abdominal cavity. As soon as the carcass sinks back to the bottom, it disintegrates rapidly and most skeletal remains are scattered across the sediment and lost due to wave action or currents (Schäfer, 1972). This might be the reason why no other skeletal remains, even teeth, were found in association with the jaws. The jaws probably have been transported after decay of soft tissues and disarticulation. However, as there is not any evidence of abrasion, horizontal transport might have been limited. The palatoquadrate and Meckel's cartilage were found in close association. Therefore, the mandibular articulation should have been intact at the moment of burial, and as the ligamentous connections decay very fast after death (Schäfer, 1972; Holz and Simões, 2002), the residence time on the seafloor should have been short. This rapid burial allowed the isolation of the jaw from destructive biostratinomic processes like scavenging, fragmentation due to transport, and bioerosion (Martin, 1999; Schäfer, 1972).

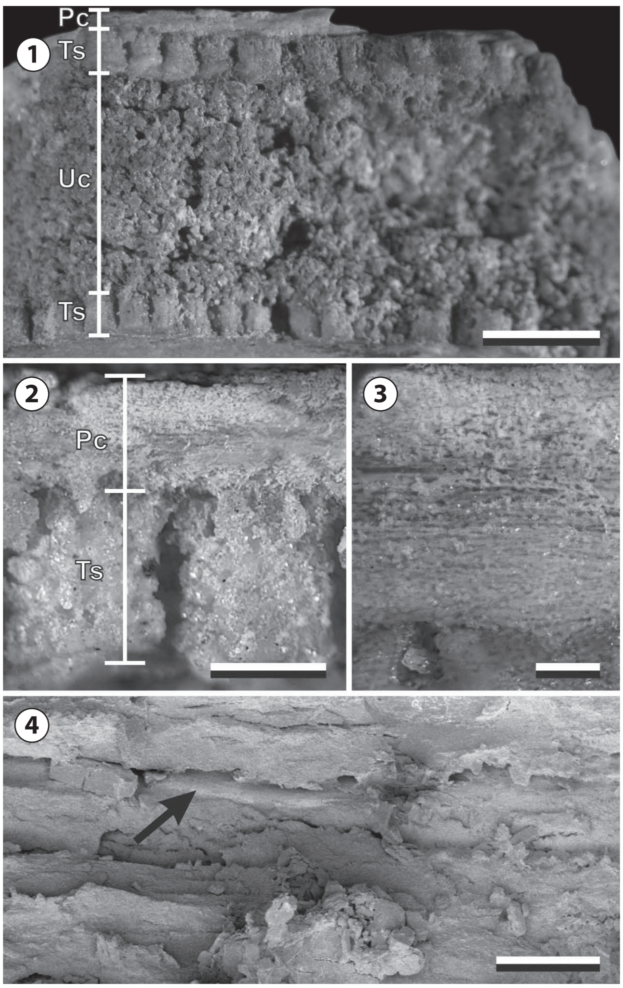

Figure 4. Tessellated cartilage of the palatoquadrate (MPEF-PV 3804)/ *cartílago teselado del palatocuadrado (MPEF-PV 3804).* **1,** general view in cross section. Scale bar= 2.5 mm/ *vista general en sección transversal. Escala= 2,5 mm;* **2,** Detail of tesserae and perichondrium. Scale bar= 500 µm/ *detalle de las teselas y el pericondrio. Escala= 500 µm;* **3,** Detail of the perichondrium showing the linear arrangement of the perichondral fibers. Scale bar= 200 µm/ *detalle del pericondrio mostrando la distribución lineal de las fibras pericondrales;* **4,** Detail of a perichondral fiber (arrow), under SEM. Scale bar= 20 µm/ *detalle de una fibra pericondral (flecha), bajo MEB. Escala= 20 µm*. **Pc,** perichondrium/ *pericondrio;* **Ts,** tesserae/ *teselas;* **Uc,** uncalcified cartilage zone/ *zona del cartílago no calcificado.*

Above the tesserae, there is a layer of well-developed mineralized tissue, which has a linear arrangement and a fibrous appearance as the perichondrium (Fig. 4.2–4). The perichondrium is a connective tissue composed by bundles of collagen fibrils and elastic fibers and is attached to the outer surface of the tesserae (Egerbacher *et al.,* 2006). This tissue has not been shown to calcify (see Kemp and Westrin, 1979; Dean and Summers, 2006) and there is not any mention in the literature of mineralized perichondrium neither in fossils nor extant sharks. As the well oxygenated environment favor the decay of unmineralized tissues by aerobic degradation, we interpret that the perichondral fibers might have been mineralized while the shark from Puerto Madryn was alive and that the mineralized perichondrium avoided the disarticulation of the tessellated tissue during decay.

The jaws are preserved without any indication of flattening. Briggs (1990) mentioned some factors that determine the nature and degree of flattening, including size and composition of sediment (coarser-grained sediments are more resistant to compaction) and the infilling of cavities. In the fossil described here, the inner core is filled with sandy sediments with similar lithological composition of the fossil bearing level. The filling of the inner core should have been immediately after (or even simultaneous with) the decay of the unmineralized cartilage. Otherwise, a hollow jaw with only the tessellated tissue could have collapsed under the weight of the overlying sediment.

In sum, this specimen represents the first tessellated cartilage three dimensionally preserved from Argentina and the first record of mineralized perichondrium. A rapid burial, the rapid filling of the inner core, and the low sediment compaction of sands have allowed the exceptional preservation of the jaws. The presence of mineralized perichondrium represents a previously unappreciated avenue by which the elasmobranch skeleton might be strengthened and reinforced. The possibility of this being common should be studied in extant species.

ACKNOWLEDGEMENTS

We thank the Agencia Nacional de Promoción Científica y Tecnológica, Consejo Nacional de Investigaciones Científicas y Técnicas, and Universidad Nacional de La Plata for financial support. The Centro Nacional Patagónico (Puerto Madryn) and the Museo Egidio Feruglio (Trelew) are acknowledged for providing the material. We also thank M. Manceñido (Museo de La Plata), the editor A. Forasiepi and the reviewers M. Dean and J. Kriwet for their helpful suggestions that improved the manuscript.

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doi: 10.5710/AMGH.v49i1(469)

Recibido: xxx

Aceptado: xxx