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*RESEARCH & KNOWLEDGE*

**Research Article**

# Revision of the fossil batomorphs from the Cretaceous of Lebanon, and their impact on our understanding of the early step of the evolution of the clade

Georges Kachacha[1,*], Gilles Cuny[2], Dany Azar[3] and Pierre Abi Saad[4]

[1]Department of EvoGenomics, Natural History Museum of Denmark, Copenhagen, Denmark
[2]UMR CNRS 5276 ENS LGLTPE, Université Claude Bernard Lyon 1, Université de Lyon, Villeurbanne Cedex, France
[3] Natural Sciences Department, Faculty of Sciences 2, Lebanese University, Fanar, Lebanon.
[4] Memory of Time, Byblos, Lebanon

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**Abstract -** Lebanon is endowed with its outstanding preservation lagerstätten of fossil fish from the Upper Cretaceous. The batomorphs are represented by 16 species of Rajiformes belonging to 9 genera and 4 families however, their phylogeny remains poorly understood. Also, their diversity is possibly underestimated, compared to the great diversification event observed in the Upper Cretaceous, by lumping the majority of Lebanese rhinobatids in the genus *Rhinobatos*, whereas their relationships with the modern species of this genus are unclear. We discuss herein the attribution of three lebanese shark-like "Rhinobatids" species included into two new genera to Rhynchobatidae. These species together with *Rhynchobatus* possess a combination of primitive characters such as propterygium failing to reach the level of the nasal capsules and pectoral fin posterior corner not reaching the level of the pelvic fin. Three additional characters are supporting this clade in the present analysis together with two plesiomorphies. The remaining guitarfishes present a closer relationship with Rajidae than to Pristidae and so the order Rhinopristiformes recently erected by Naylor et al., (2012) is not recovered in our analysis.

**Keywords:** Batomorpha, Upper Cretaceous, Rhinobatidae, cladistics

## 1. Introduction

The Superorder Batomorpha (skates, stingrays and their allies) presents the largest taxonomic diversity among extant chondrichthyes (≈630 of ≈1221 species) (Compagno, 2005; Fowler, 2005; Naylor *et al.,* 2012). It appeared during the Jurassic (Underwood, 2006) and is divided into three orders: Rajiformes, Myliobatiformes and Torpediniformes (Cappetta, 2012). This cartilaginous fish lineage is recognized as a monophyletic group sister to all living sharks (Selachimorpha), based on both molecular and morphological data (Douady *et al.,* 2003; Maisey *et al.,* 2004; Winchell *et al.,* 2004; Aschliman *et al.,* 2012a; Naylor *et al,* 2012; Carvalho, 1996). Nonetheless, the interrelationships within batomorphs remain controversial amongst morphologists and molecular biologists, with the most contentious issues concerning the most basal group position. The phylogenetic relationships within batomorphs are yet even more complicated when fossils are considered because their fossil record is mostly restricted to teeth, dermal denticles and occasionally, fin spines and calcified vertebrae. Thus, the position of the Sclerorhynchoidei and the Jurassic and Cretaceous guitarfishes (like *Spathobatis*, *Belemnobatis* and several fossils Rhinobatoids) in the phylogenetic tree of batomorphs and within Rajiformes is far from clear.

In the Upper Cretaceous of Lebanon, the batomorphs are represented by 16 species of Rajiformes belonging to 9 genera and 4 families. The Rajiformes phylogeny remains poorly understood with the "Rhinobatidae" forming a polyphyletic group (Brito and Dutheil, 2004; Brito *et al,* 2013; Claeson *et al*. 2013) and the position of the Sclerorhynchoidei fluctuating due to the lack of available well-preserved specimens. Similarly, the phylogenetic affinity of the Lebanese fossil Rajidae and Cylobatidae is not yet solved. The diversity of the Lebanese Rajiformes is possibly underestimated, compared to the great diversification event observed in the Upper Cretaceous (Guinot and Cavin, 2015), by lumping the majority of Lebanese rhinobatids in the genus *Rhinobatos*, whereas their relationships with the modern species of this genus are unclear (Cappetta, 2012; Claeson *et al,* 2013; Brito *et al.,* 2013).

The outstanding preservation lagerstätten of the newly found complete rhinobatid taxa from the Upper Cretaceous of Lebanon allows the possibility of integral

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[*]Author for correspondence: georges.kachacha@snm.ku.dk

anatomical exploration of the studied fossil organisms. Subsequently, complete redescriptions for these species were undertaken and will constitute together with a full analysis of their affinities the subject of forecoming publications. However, we discuss herein the attribution of three shark-like "Rhinobatids" species to Rhynchobatidae and how the remaining guitarfishes are not related to other recent species *Rhinobatos*.

## 2. Material and method

Lebanon, which was located in the North East part of Gondwana during the Late Cretaceous, is endowed with several Konservat-Lagerstätten that have yielded a variety of excellently preserved fossils (Philip *et al.,* 1993). The best known Lebanese fossil localities are Haqel (حاقل), Hjoula (حجولا) and Nammoura (نمورة) from the Cenomanian, and Sahel Aalma (ساحل علما) from the Santonian (Davis, 1887; Cappetta, 1980).

The Phylogenetic affinities of 15 batomorph taxa from the Lebanese outcrops (including two new species with exclusion of two Sclerorhynchids species) have been performed based on type material and additional well-preserved and complete material. The latter material was provided by "Memory of Time" private collection whereas some specimens were purchased or donated to the Natural History Museum of Denmark or to the Lebanese University. A set of 65 morphological characters (among which 11 are new) were used in a cladistic phylogenetic study based on 36 taxa. The matrix was compiled using Mesquite 3.10 (Maddison and Maddison, 2010) and the parsimony analyses were performed using TNT 1.5-beta (Goloboff *et al.,* 2003).

## 3. Results and discussions

The topology of this analysis is in general agreement with the previous analysis of Brito and Dutheil (2004) and Claeson *et al.,* (2012), with a better resolution for the affinities of the Lebanese guitarfishes. Nonetheless, it presents marked discrepancies in the relative positions of batomorph clades with other studies based on different phylogenetic methods. The torpediniforms are recovered as sister group to all batoids in the morphological analysis of McEachran and Aschliman (2004), Aschliman *et al.* (2012b) and Claeson *et al.* (2012) as well as in the molecular analysis of Rocco *et al.* (2007) and Rocco (2013). On the other hand, Rajids are considered the ancestral group of all batoids in the molecular study of Aschliman *et al.* (2012a) and Naylor *et al.* (2012). Our analysis is in agreement with the morphological studies of Shirai (1996) and Brito and Dutheil (2004) as well as the molecular study of Pavan-Kumar *et al.* (2014) in considering the shark-like guitarfish as sister group to all batoids.

Three shark-like "Rhinobatids" from Lebanon, *Gen nov. 1 grandis* (Fig. 1a), *Gen nov. 1 maronita* (Fig. 1b) and *Gen nov. 2 tenuirostris* are united together within a clade including *Rhynchobatus*, as found in Brito and Dutheil (2004) and Claeson *et al.,* (2012), with the exclusion of *Pristis*, *Spathobatis* and *Sclerorhynchus*. These two new genera present two out of the three characters identified by Nishida (1990) (propterygium failing to reach the level of the nasal capsules; pectoral fin posterior corner not reaching the level of the pelvic fin) for which Rhynchobatidae exhibit plesiomorphic state relative to the most other batoids. The third characters regarding the caudal fin presenting well- differentiated dorsal and ventral lobes, is only marked for *Gen nov. 1 grandis*. This character is missing in *Gen nov. 2 tenuirostris* (holotype lacking the extremity of the tail) and not scored for *Gen nov. 1 maronita* that presents a slender caudal fin with a well developed dorsal lobe.

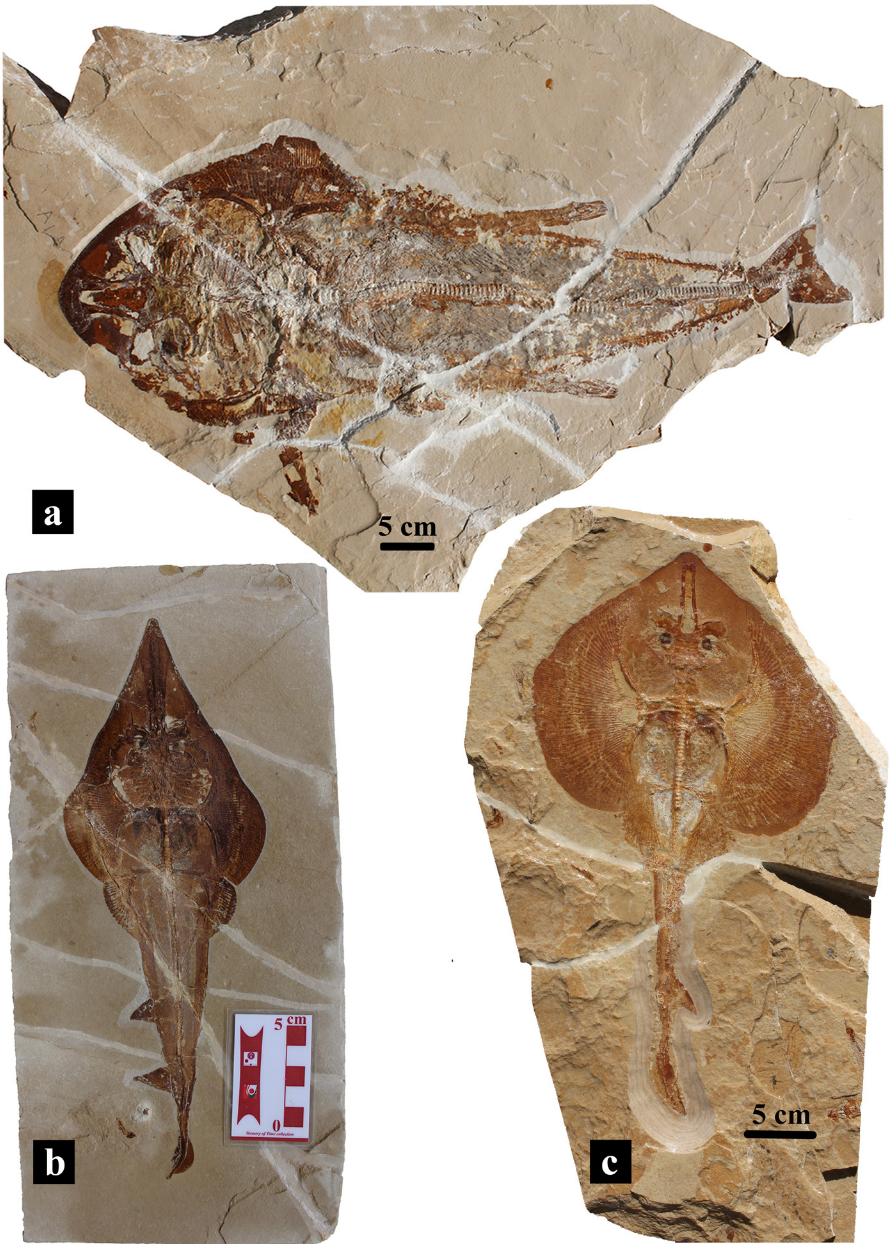

**Figure 1.** Habitus for guitarfishes from the Upper Cretaceous of Lebanon. (a) *Gen nov. 1 grandis*, well-preserved male in dorsal view from Haqel (LB-V-2015-01); (b) *Gen nov. 1 maronita*, well-preserved and complete male in dorsal view from Haqel (NHMD-74748); (c) *Gen nov. 3 B nov.*, holotype in dorsal view from Hjoula (LB-V-2016-01).

Three additional characters (rostrum representing more than two third of the total neurocranium length; teeth with well-developed median uvula; pectoral radials all articulating with pro, meso and metapterygium) are supporting this clade in the present analysis together with two plesiomorphies (presence of horn-like anterior processes; presence of labial cartilages). Thus, the two new *genera Gen nov. 1* and *Gen nov. 2* are excluded from Rhinobatidae family and assigned to Rhynchobatidae. *Gen nov. 1* is recovered as sister group to *Gen nov. 2* based on two characters (rostral appendices covering at least half of the rostrum; pectoral radials extending as far as the level of the nasal capsules) with the addition of three plesiomorphies (antorbital cartilage directly jointing the inner rostral most part of the propterygium; teeth with sharp transverse crest that rises centrally into an obtuse and low angle or cusp; posterior section of the propterygium extending behind the procondyle). *Gen nov. 2 tenuirostris* and *Rhynchobatus* are recovered in one clade and sister to *Gen nov. 1* based on two characters (rostral appendices covering the distal third of the rostrum; pectoral radials extending not reaching the level of the nasal capsules) with the addition of one plesiomorphic character (radials of the mesopterygium are made of three undivided segments and the dichotomy is located at the half of the pectoral fins length). *Gen nov. 1* present two dorsal fins those unlike Rhynchobatidae are caudally located to the pelvic fin. In a result, the Rhynchobatidae family definition needs to be reassessed.

The crown guitarfishes are recovered as sister group to rajids in the 50% majority rule tree based on one synapomorphic character (occipital condyles wider than the base of the synarcual lip) in addition to five characters (presence of labial cartilages; ribbed dorsal groundmass denticles; absence of alar and/or malar thorns; placoid scales uniformly present; suprascapulae articulated with vertebral column) and one plesiomorphy (rostrum length less than two third of the total neurocranium length). This clade on the top of the tree including the crown guitarfishes together with rajids is supported by one synapomorphy (propterygium extending as far as the level of the nasal capsules) in addition to three plesiomorphies (anterior fontanelle tabular in shape and stops before reaching the rostrum extremity or at the level of the rostral appendices base; the antorbital cartilage is joining the inner margins of the propterygium; pectoral radials extending far beyond the level of the nasal capsules). As a result, the order Rhinopristiformes recently erected by Naylor *et al.,* (2012) is not recovered in our analysis where the crown group of "Rhinobatidae" presents a closer relationship with Rajidae than to Pristidae. The crown Lebanese guitarfishes *Gen nov. 3* (*Gen nov. 3 hakelensis*, *Gen nov. 3 whitfieldi* and *Gen nov. 3 B nov.* (Fig. 1c)) and *Gen nov. 4* (*Gen nov. 4 latus* and *Gen nov. 4 intermidius*) are recovered in two resolved clades in a polytomy with *Rhinobatos*, *Trygonorrhina* and *Zapteryx,* where all are rooted by *Iansan* and *Aptychotrema*. *Rhinobatos* is excluded from the crown Lebanese guitarfishes in the strict consensus tree and based on two characters (pectoral propterygium not reaching the level of the nasal capsules; tail with stocky appearance and representing half of the total body length). *Gen nov. 3* is supported by three characters (antorbital cartilage free from the propterygium; teeth with incipient lateral uvulae; posterior section of propterygium extending behind procondyle) whereas *Gen nov. 4* is supported by two characters (nasal capsules with a horn-like anterior process; teeth with flat crown and lacking shark transverse crest). However three additional characters (pectoral radials extending as far as the level of the nasal capsules; proximal segment of the propterygium is rostrally to the jaws level; radials of the mesopterygium are made of three undivided segments and the dichotomy is located at the half of the pectoral fins length) provide ambiguous support for a clade including *Gen nov. 4* as sister-group to *Rhinobatos* in the 50% majority rule tree. Therefore, the monophyly of Rhinobatidae is not recovered and the assignment of *Gen nov. 3* and *Gen nov. 4* to "Rhinobatidae" is considered as doubtful.

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