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Fossil marlins (family Istiophoridae) from the Piña locality (Panama; Chagres Formation; Miocene) – morphology and comparison with related forms

Fosilní mečouni (čeleď Istiophoridae) z lokality Piña (Panama; souvrství Chagres; Miocén) – morfologie a srovnání s příbuznými formami

Diploma thesis

Advisor:
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Declaration:

I declare that I worked by myself in all parts of this thesis and that I have included here all sources of information and literature. Neither this work nor any substantial part of it has been used for the acquisition of other academic title or equivalent.

In Prague, 15. 5. 2017

Carlos DeGracia

Dedicated to my parents and family

AKNOLEGMENTS

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ABSTRACT

The study of fossil istiophorids is limited by its fragmentary fossil record; the absence of osteological specimens for comparisons; the cryptic bibliography of several early works and the absence of more accurate comparative methods. Appling a data imputation model we took advantages of extant data for rostral and articular variables for istiophorid billfishes. We used this result to apply PCA analysis and we compared fossil and modern istiophorids together. With this analysis we present here two new istiophorid species: *Makaira*? sp. nov. 1 and *Makaira* sp. nov. 2. *Makaira*? sp. nov. 1 is the most complete fossil istiophorid ever discovered and represent that share characters in various genera. We hypothesize that characters in bones involved in alimentation process have phylogenetic importance as: rostrum shape, denticles, lower jaw, vomer, basioccipital and skull shape as well as orbital size. Our taxonomic reviews of fossil istiophorid reorganize its taxonomy and solve many conflicts about the classification of fossil species. The istiophorids are abundant macrovertebrate in the Chagres sediments and its presence suggests a water column with a minimum of 200m depths in an environment of short platform with oceanic influence. Given the high productivity inferred in this environment we suggest that istiophorid aggregation in the Late Miocene of Chagres Formation could be seasonal and that they could use the Central American Seaway as migration route before the modern oceanographic pattern were established.

ABSTRAKT

Informace o fosilních zástupcích čeledi Istiophoridae jsou limitovány zejména jejich fragmentární povahou; chybějícím kosterním materiálem využitelným při srovnávacích studiích; nedostupností vybrané historické literatury a absencí vhodných srovnávacích metod. S využitím metody "Data Imputation" byla doplněna stávající data izolovaných roster I artikulovaných exemplářů istiophoridních mečounů. Výsledek byl analyzován metodou PCA a srovnán s fosilními i dnešními zástupci čeledi Istiophoridae. Analýza jasně ukázala existenci dvou nových druhů čeledi Istiophoridae: *Makaira?* sp. nov. 1 a *Makaira* sp. nov. 2. Exemplář klasifikovaný jako *Makaira?* sp. nov. 1 je doposud nejkompletnější známý fosilní istiophorid sdílející znaky několika rodů. Je předložena hypotéza, že znaky na kostře související s adaptací k lovu mají fylogenetický význam, například tvar rostra, dentikuly, spodní čelist, vomer, basioccipitale, celkový tvar lebky a velikost orbity. Předložená taxonomická revize fosilních istiophoridů reviduje jejich taxonomické zařazení a řeší řadu historických problémů týkajících se jejich klasifikace. Istiophoridní mečouni jsou častou makrofosilní složkou v sedimentech souvrství Chagres a jejich přítomnost naznačuje hloubku minimálně 200 m a prostředí platformy s oceánskými vlivy. Vzhledem k produktivitě prostředí lze předpokládat, že akumulace istiophoridů v sedimentech souvrství Chagres v období pozdního miocénu byl sezónní a prostor byl využíván jako migrační cesta před ustanovením moderního oceánického uspořádání.

CHAPTER ONE

INTRODUCTION

1.1 The istiophorid billfishes

The Marlins and spearfishes (Istiophoriformes: Istiophoridae) refer to fishes with their prenasal and premaxillar bones elongated and fused distally forming a "rostrum" or "bill" covered by villiform teeth (Schultz 1987; Fierstine 1990, 2006; Fierstine & Monsch 2002). They have scales present in adults; pelvic fins elongate; caudal peduncle (in adult) with two keels on each side; the dorsal fin has very long base (sometimes sail-like), depressible into a groove and lateral line retained throughout life (Nelson 2016). Marlins (Istiophoridae) differ from other Istiophoriformes by following outapomorphies: prenasals are included in the posterior half of the rostrum; rostrum is round to oval in cross-section with one pair of lateral longitudinal nutrient canals; lower jaw with a toothed predentary at the distal tip; and 24 vetrebrae mostly interlocking neural and hemal spines and zygapophyses to form stiff unit (Fierstine 2006; Nelson 2016). Modern marlin includes five genera: *Istiompax* (1 species), *Istiophorus* (1 species), *Kajikia* (2 species), *Makaira* (1 species), *Tetrapturus* (4 species), with 9 species in total (Nelson 2016), but some authors divides originaly monotypic *Istiophorus platypterus* in *I. platypterus* and *I. albicans* based in differences in the lateral line and DNA sequences; and recognize additional and unnamed species of *Tetrapturus* with molecular analysis (e.g. Nakamura 1983, 1985; Collette *et al.* 2006).

Modern marlins (Istiophoridae) are big size fishes (up to 4 m with a weigh records of 820 kg) and exceptionally fast swimmers achieving burst speeds of up to 81 km/h and sustained speeds of 29–43 km/h in the blue marlin *M. nigricans* (Block *et al*. 1992; Peperrell 2010). They are primarily oceanic, epipelagic species inhabiting tropical and temperate waters, and seasonally also the cold waters of all the oceans. Usually, billfishes are confined to the water layers above the thermocline, but some may occur at greater depths (bellow 800m; Collette *et al*. 2006; Pepperrel 2010). However, marlins inhabit principally tropical waters (where are found its major concentrations) and are less abundant in temperate regions (Arrocha & Ortiz 2006; Peperrell 2010). The biggest marlins species has a wide distribution range and are able to do interoceanic and transoceanic migrations to find food spots and spawning areas where they do seasonal aggregations in open–ocean environments where they prefer ocean waters over continental shelves, waters around drop–off reefs, open ocean islands and far away atols (Ortiz *et al*. 2003; Orbesen *et al*. 2008; Pepperell 2010).

1.2 The fossil record of istiophoridae

The fossil record of marlins tentatively goes back from the late Eocene to the Pleistocene (Fierstine 2006) whit six extinct species described principally by nearly complete rostra: *Istiophorus solidus* (Van Beneden, 1871), from the late Eocene of Belgium; *Makaira belgicus* (Leriche, 1926) from the middle Miocene of Belgium; *Makaira teretirostris* (Van Beneden, 1871) from the middle Miocece of Belgium; *Makaira courcelli* Arambourg 1927, from the early Pliocene od Algeria; *Makaira panamensis* Fierstine, 1978, form the late Miocene of Panama and *Makaira purdyi* Fierstine, 1999a, from the early Pliocene of North Carolina. Some of this fossil fossil species should be reconsidered in sense of higher classification, taxonomically revised and data regarding type localities verified. For example *I.*

solidus may be not an Istiophorid (Shultz 1987), the type specimen of *M. teretirostris* is missed (and such hardly verifiable) and *M. courcelli* present distinctive external shape and internal anatomy by having one nutrient channel in the anterior part of the rostrum and two in the distal part (Arambourg 1927; Shultz 1987; Fierstine 1978, 2001b, 2006).

Additionally to the extinct species mentioned above there are several fossil records of extant marlins species that are represented mostly by fragmented rostra found in USA, Mexico, Italy, Spain, Panama, Chile and Philippines. These fossils have been recovered principally from sediments with estimated paleobatymetric ranges from middle to depth waters (Gottfried 1982; Schultz 1996; Fierstine 1978, 1998, 2001, 2008; Fierstine & Welton 1983; Fierstine *et al*. 2001; Carnevalle *et al*. 2002). Despite billfishes are more common in tropical oceans, the fossil record are principally limited to temperate zones and the only records from tropical zones are in Panama and Philippines (Fierstine 1978, 1999b, Fierstine & Welton 1983; Pepperrel 2010). This situation, combined with the fragmentary condition (mostly rostrums fragments), make difficult to understand its evolutionary history and the paleobiogeography (Fierstine 1978, 1999b, Fierstine & Welton 1983; Pepperrel 2010). Although ichthyologists have made great efforts to understand the origin and diversification and evolutionary history of modern marlins still there are no evidence that combines data from modern and fossil species in one analysis.

Here we describe a new species of marlins from the Late Miocene of Chagres Formation in Panama. The specimen represents a huge 2.66 m new fossil marlin: *Makaira?* sp. nov. specimen STRI 31291, and *Makaira* n. sp. 2 STRI 31293, both collected in the Chagres Sandstone from the Late Miocene of Chagres Formation in the Caribbean coast of Panamá. The specimen STRI 31291 is articulate and its extraordinary preservation includes cranium, vertebral column and fins. Additionally, a review of all extinct fossil Istiophorids is presented and a standardize terminology to describe fossil istiophorids is introduced in this work. *Makaira?* sp. nov. is the biggest and best informative fossil istiophorid known up to date and represents an evolutionary transition state by sharing characters between *Makaira*, *Istiophorus* and *Tetrapturus*.

1.3 Locality and stratigraphy

The Chagres Formation is the youngest formation from the Panama Canal Basin (Coates 1999) and was originally named by Macdonald as result of the Geological surveys during the Panama Canal construction (Macdonald 1915). Has a thickness of approximately of ~250 m and the outcrops are only exposed at the northern end of the basin on the Caribbean coast (Fig. 1). The unit overlaps disconformably on Gatun Formation and consisting predominantly of marine and an arc-derived, volcanoclastic sandstone with an age interval from 8.6 to 5.3 Ma (Collins *et al.* 1996; Coates 1999). The sediments consist of indurated, conglomeratic, coarse-grained, volcanic sandstone with quartz, feldspar, lithic grains, with abundant bioturbation and is divided in tree members: Toro, Rio Indio and Chagres Sandstone (Coates 1999) (Fig. 1).

The Toro member is the stratotype of Chagres Formation and is exposed between Toro Point and Naranjitos Point (Fig. 1). Toro member is the base of

Chagres Formation and has about 60 m of thickness and is well exposed on the cliffs at the west of Toro Point where is distinguished by a notable echinoid – mollusk – barnacle coquina (Coates 1999). This coquina represents high-energy cross-bedded with a very coarse volcanoclastic associated with bathyal Pacific benthic foraminifera that indicates strong Pacific affinity and upper bathyal depths (Carrillo – Briceño *et al*. 2015; Collins *et al*. 1999).

The Rio Indio Facies replace laterally the Toro member (Fig. 1) and Consists in a fine silty-sandstone that were deposited in shallow waters of 50 – 80 m depth (Carrillo – Briceño *et al*. 2015; Aguilera & Rodriguez de Aguilera 1999; Collins *et al*. 1996). Rio Indio according advances of our work has an age of 7.64 Ma based on ^{87}Sr/ ^{86}Sr isotopes from bivalves (Hendy *et al*. in review). This member is exposed approximately from the mouth of Rio Lagarto to Punta Mansueto (Fig. 1).

The youngest member is the Chagres Sandstone, which are principally exposed in cliffs from the mouth of the Chagres River in west direction to approximately the mouth of Rio Caño Quebrado (Fig. 1). We call informally this member "Piña facies" (Fig. 2 - 3), and consists of grey volcanic, quartzose, with lithic and feldspar grains silty-sandstone, with pervasive bioturbation of arthropod burrows with 5-10 cm of diameter (Coates 1999) (Figs. 2 - 3). The Chagres Sandstone is a fossiliferous member with abundant macro invertebrates (such as thin disarticulated bivalves, fragmented gastropods, squid beaks and urchins) (Hendy *et al*. in review), micro invertebrates (as benthic foraminifera) (Collins *et al*. 1996) and a rich marine – well preserved vertebrate fauna previously unknown and discovered by the author that consists in abundant remains of chondrichthyans (Carrillo *et al*. 2015), fish otoliths (De Gracia *et al*. 2012; Schwarhanz & Aguilera 2013) fish bones (Fierstine 1978) and cetaceans (Vigil & Laurito 2014; Velez – Juarbe *et al.* 2015; Pyenson *et al.* 2015) (Fig. 2). According Woodring (1957) and Collins *et al.* (1996), the mollusks and foraminifera found in Chagres Sandstone member indicates strong Pacific affinity in this Caribbean Formation.

The Piña locality (9° 16' 53.4'' N, 80° 2' 40.9'' W) is a locality in the Chagres sandstone member located on the coastline near to the Piña Town, Chagres district, Colon province, Panama (Fig. 1 - 3). The outcrops are located along prominent cliffs from the mouth of Piña river to ~3.6 km to SW of the town (Fig 1). The outcrops are only available when the tide is low making difficult and extreme the conditions to excavate fossil vertebrates (Pyenson *et al*. 2015). This condition reduces the available time to do vertebrate excavation before the ocean is covering fossils again. This is one of the reasons why any paleontologists have not found this fossiliferous layer in previous expeditions since Chagres Formation was described and the only vertebrate was *Makaira panamensis* Fierstine, 1972.

1.4 Objectives

The primary objective of this thesis is to describe a new fossil istiophorids from the Chagres Formation in the Caribbean of Panama using a combination of descriptive methods established in previous works (Fierstine 1998, 2001; Fierstine & Voight 1996) and quantitative PCA analysis. Despite modern istiophorid billfishes are well studied in the fossil record they are poorly understood and there is a necessity of standardize the terminology used to facilitate the fossil species description. Following this way the second objective is to propose a new terminology for describe fossil billfishes based in the internal anatomy of the cross – sections of the bill and the distal shape of the bill tip. We also present a detailed review of all fossil istiophorid species knows to the date. Finally there is some confusion about type localities and description of some fossil species that need to be reviewed in detail using type specimens and original literature because we detect some information lack in our research. The third objective is to present a complete taxonomic review of all fossil istiophorids. Finally we discuss about istiophorid – billfishes evolution and its paleobiogeography.

CHAPTER TWO

METHODOLOGY - OVERVIEW

2.1 Overview

To describe fossil billfishes, we followed the methodology used by Fierstine & Voight (1996) and Fierstine (1998, 2001). Additional characters as neurocranium shape, vomer shape and vertebra 14 were studied following the methodology of Nakamura (1983). We used a combination of osteological terminology of Gregory (1933), Gregory & Conrad (1937), Jollie (1986), Schultz (1987), Davie (1990) and Rojo (1991), and. Linear measures of bones were made to the nearest 0.5mm with dial calipers or tape – measure and using Computer Tomography when is indicated. We followed the taxonomy of Nelson *et al*. (2016) for the classification of the fossil material. To support our taxonomical identifications we included parametric statistics using Principal Component Analysis (PCA). The specimens presented in this thesis were collected in October 2011 by the Smithsonian Tropical Research Institute (STRI) – Center of Tropical Paleontology and Archeology (CTPA) paleontologist crew in the beach of Piña Town in Colon, Panama (Fig. 1, 3). These fossils have been cataloged as STRI 31291 and STRI 31293 in the paleontological collection of STRI. The specimens were prepared mechanically with carbon fiber needles, airscribes chisels and rotatory flexible shafts tools; and chemically with hydrogen peroxide solution at 10% in the CTPA by the author.

2.2 Comparative material

Comparative modern material: *Xiphias gladius* (Swordfish): USNM 110042 entire skeleton; *Istiophorus platypterus* (sailfish): STRI archeology collection 1628 entire skeleton, MNHN A-9463 skull, MNHN A-9464 skull, MNHN 6960 complete skeleton; *Makaira nigricans* (blue marlin): USNM 196019 entire skeleton, LACM 46023-1 vertebral column, MNHN 1892-1050 rostrum; *Istiompax indica* (black marlin): LACM 25509 entire skeleton, UF 210017 pectoral girdle, MNHN 1884.29 pectoral fin, MNHN A-5514 rostrum fragment, MNHN 2003-0420 complete dry specimen; *Kajikia albida* (white marlin): USNM 270766 skeleton, USNM 3605507 axial skeleton; *Kajikia audax* (striped marlin): USNM 372777 entire skeleton, MNHN 6821 entire skeleton, LACM 25500 skull; *Tetrapturus pfluegeri* (long bill spearfish): LACM 25462 entire skeleton, UF-208789 vertebral column and pectoral fin girdle; *Tetrapturus belone*: MNHN A-7504 entire skeleton; *Tetrapturus angustirostris* (short bill spearfish): LACM 25499 entire skeleton.

Comparative fossil material: *Istiophorus solidus* (holotype): IRSNB P643 rostrum; *Makaira belgica* (holotype): IRSNB P117; *Makaira courcelli* (holotype): MNHNP 250; *Makaira panamensis* (holotype): USNM 18710; *Makaira purdyi* (holotype): USNM 481933.

2.2.1 Institutional abbreviations: **STRI**, Smithsonian Tropical Research Institute, Panama, city of Panama; **CTPA**, Center of Tropical Paleontology and Archaeology of STRI, Panama, city of Panama; **USNM**, Smithsonian National Museum of Natural History, Washington D.C., U.S.A., **UF**, Florida Museum of Natural

History, Gainesville FL., U.S.A.; **LACM**, Natural History Museum of Los Angeles Country, Los Angeles C.A., U.S.A.; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique; **MNHN**, Museum National d'Historie Naturelle (Paris); **HSF**, Hospital Santa Fe, Panama, city of Panama.

2.2.2 Anatomical abbreviations: **A**, articular; **BO**, basioccipital; **D**, dentary; **DE**, dermothmoid; **EP**, epihyoid; **EPU**, epural; **EX**, exoccipital; **F**, frontal; **FP**, first pectoral fin ray; **H**, hypural; **i pr**, internal process; **LE**, lateral ethmoid; **mf**, mandibular foramen; **m pr**, maxillary process; **N**, nasal; **OP**, operculum; **ORB**, Orbita; **P**, epiotic; **PA**, parasphenoid; **PD**, predentary; **PM,** premaxilla; **PN**, prenasal; **PO**, Posttemporal; **PRO**, Prootic; **PT**, pterosphenoid; **PTO,** Pterotic; **Q-A**, socket for quadrate – articular joint; **rs**, rib socket; **sf**, spinal foramen; **SO**, suboperculum; **SP**, sphenotic; **SU**, supracleithrum; **V**, vertebra **Vo**, vomer; **tr**, triangular region of the maxilla. Here we also includes abbreviation for right side; **R** and for left side; **L.**

2.3 Characters

Rostral fragments are the most common istiophorid fossil material and Fierstine developed the methodology to identify fossil billfishes using rostral characters and compare it with extant species (Fierstine & Voight 1996; Fierstine 1998, 2001). We will mention quickly the variables used in this work but a detailed description of all variables and methodology is available in Fierstine 1998, 2001.

Rostrum (Figs. 4 – 5a-b): Two regions were emphasized for the fossil specimens: 0.5L (one –half the distance between the distal tip and the orbital margin of the lateral ethmoid bone) and 0.25L (one-fourth the distance between the distal tip and the orbital margin of the lateral ethmoid bone) (Fig. 4). Characters studied in each region were depth (D1, D2) and with (W1, W2) of the rostrum, height (H1, H2) and with (N1, N2) of left nutrient canal, distance (DD1, DD2) of the nutrient canal from the dorsal surface and distance between canals (IC1, IC2) (Fig 5 a-b). Characters without region reference were position of prenasal bone from the distal tip of the rostrum (P) and length from tip to where the fused premaxillaries divide (VSPM) in two separate bones (Fierstine 1998, 2001) (Fig. 4).

Neurocranium (Fig. 5c): three characters were taken of the neurocranium: ACW, anterior cranium width measured on the front edge of the vomer, PTW, anterior cranium with at pterotics and CAL (or CL), cranium length from the exoccipital to the front edge of the vomer in ventral side (Fig. 5c) (Nakamura 1983).

Dentary (Fig. 6a): Two character are in the interdentary joint: DAD, depth from the anteriormost denticles to the ventral margin; and DJL, length of the interdentary joint from the mandibular foramen to the anteriormost denticles (Fierstine 2001).

Vertebra 14 (Fig. 5d-h): three characters are in the vertebra 14: CL, length of centrum; NH, height of neural spine and NL, length of the neural spine (Fig. 5d) (Nakamura 1983).

Vertebra 22 and 23 (Fig. 6b): AS, length of the anterior edge of the centrum to the anterior margin of the spinal foramen; PS, length from the posterior edge of the centrum to the posterior margin of the spinal foramen; CL, length from the anteriormost edge to the posterior edge of the centrum; VPD, dorsoventral diameter of the anterior surface of the centrum (Fierstine 2001).

Articular (Figs. 6c-d): Five characters were studied in the socket region: ASM, length of the socket from its anterior posterior margin; AL, length of the socket from its anterior to its posterior margin; AAL, length from the apex to the posterior margin; ATW, with of the socket region from the medial process to the outer margin; AW, with of the socket proper (Fierstine 2001).

First pectoral fin ray (Fig. 6e): FW, greatest with from the outer margin of the flange to the outer margin in the ray; and FAW, with of FW that crosses the scapular facet (Fierstine 2001).

Predentary (Figs. 6f-g): PL, length along the ventral midline; PW, with across the widest expanse of the denticulated surface and PD, depth perpendicular to the long axis from the widest expanse of the denticulated surface to the ventral surface (Fierstine 2001).

2.4 Fierstine descriptive method

For the first part, we implemented the qualitative methodology used by Fierstine (1998, 2001) and we combine it with a new terminology introduced here to describe cross-sectioned rostrums and the differencies in the distal tip for fossil istiophorids (Figs. 7 - 8). The Fierstine method indicates that the identification for fossils is accomplished by covering length and width measurements of individual bones (characters) (Figs. 4 - 6, Table 1, 6) to ratios (proportions) by dividing the shorter measure between the longer one (Table 2). We tearing ratios as variables, and comparing them to computed ratios from a series of bones from recent istiophorids species (Table 2). If a ratio fell within the range of one or more recent species it was scored for each species that contained the ratio (Tables 3 and 4). The unknown fossil should be identified as the recent species whit the most scores, unless:

1. Its overall score overlapped two or more genera
2. Its overall score overlapped two or more species at the same genus
3. Some of its scores fell out side the observed range of recent species.

In the first two cases, the unknown fossil would be identified only to genus or family, respectively. In the third case, the unknown would be identified as a known fossil species, a variant of a recent or fossil species, or a new species, depending on how it differed from the fossil or recent species. For this section we also plotted the ratios of the dentarium, vertebra 22 and vertebra 23 in a boxplot diagram to visualize the behavior of these variables in this bones and make a visual comparison between fossil and recent species.

2.5 New terminology for istiophorid – billfish identification

With a revision of the modern istiophorid specimens and all fossil species knows to the date, we include here a new terminology based in the internal anatomy of the cross section of the rostrum. With emphasis in the nutrient canals, we studied tits vertical position, the lateral distribution and the rotation of the left canal and we established a new terminology for differentiate each variation. After this revision we also include a new terminology for differentiate the variation in the distal tip of the rostrum. We expect this contribution help to standardize the description of fossil billfishes in the future.

CHAPTER THREE

METHODOLOGY - DATA ANALYSIS

For comparisons we used data from 214 istiophorids specimens distributed in 6 species. We applied the Fierstine method for billfish identification and follow we used a data imputation model for apply a PCA analysis for rostral variables and articular bone. All calculations, data analyzes and plots were generated with R system (R core team 2017). In this point we have included all data used for the analysis as supplementary information in the Table S1 for imputed for rostral variables used in the PCA for rostral variables; Fig. S1 for show the correlation levels for rostral variables and Table S2 for variables and individuals used for the PCA for articular bone

3.1 Problems with missing data for PCA analysis

Principal component is a standard technique used to summarize the main structures of a dataset containing the measures of several quantitative variables for a number of individuals (Dray & Josse 2015). PCA is often used in ecology studies with the aim to understand why individuals co – occurs in the same location, for study similarities between individuals from a multidimensional point of view and to examine effects of abiotic and biotic features on observed assemblage structures (Godall 1954; Josee & Husson 2012; Dray & Josse 2015). The standards multivariate techniques like PCA are based on the eigendecomposition of a cross-product matrix and thus require complete datasets (Dray & Josse 2015). Unfortunately, data sets often have missing values limiting the use of PCA methods by elimination of individuals with missed variables (Dray

& Josse 2015). This represent to lose several data before to implement the PCA but a solution can be to implement some data imputation method that are available in software packages for the R system prior PCA (Josse & Husson 2016).

First step is distinguishing what are the mechanisms generating missing data for our analysis (Dray & Josse 2015): missing completely at random (MCAR), missing at random (MAR), and missing not at random (MCAR) (Rubin 1976). In this case our data are MAR, this means that the probability that an observation is missed is related to the values for some other observed variables (Dray & Josse 2015). We follow this assumption because the variables we are using are morphological characters and some values are missed because the specimen lacks one or more bones. Additionally a strong correlation in our preliminary analysis (not included here) between the variables we are using express the relationship between this anatomical structures and make us think that missing values can be inferred by interrelate all others observed values.

3.2 Data imputation model

We used the Multiple Imputation PCA Method (MIPCA) that is specialized in MCAR and MAR missing values and uses a regularized version of the PCA algorithm to impute data (Josse & Husson 2012; Josse *et al.* 2011). MIPCA is a powerful tool for data imputation. Can overcome several problems involved in the process as overfitting and is available in the package "missMDA" for R system (Josse & Husson 2012, 2016; Josse *et al.* 2011). To impute data we treat each species as individual dataset. The percentage of missing values for each subset of data are the next: *I. platypterus*, 10.57%; *M. nigricans* 9.8%; *M. indica*, 18.0%; *K. albida* 32.0% and *K. audax*, 30.0%. The first step consist in calculate the number of dimensions (ncp) required for the regularized PCA algorithm prior to apply the MIPCA. To do this we used the function “estim_ncPCA” for each subset of data. We used the regularized version of the interactive PCA algorithm and cross – validation method “K – fold” to test a minimum of 0 and a maximum of 6 components. The percentage of missing values inserted and predicted with PCA where 0.05% for a total of 100 simulations. This step is critical because few dimensions in the PCA algorithm lead to loss information and to many lead to overfitting problems (Josse & Husson 2012).

After get the recommended number of dimension for each subset of data we applied the multiple imputation to the data using the function “ MIPCA”. We used a regularized version of the Interactive PCA algorithm as method for 200 imputed datasets. In this model the observed values are the same but imputed values differs for each imputed dataset (Josse & Husson 2016). As this is a multiple imputation, the variance of prediction consists in two parts: (1) the variability in the estimated values of the PCA parameters and (2) the variability due to the noise (Jose & Husson 2016). To obtain the variance of the parameters we used Bayesian approach for this model. When each data subset was imputed we merged together all imputed data in the supplementary information (Table S1). We should mention that data of *K. audax* were imputed without the variable DD1 because the variable is completely missed for this species (Table S1).

3.3 Rostral variables for cross - section area

Next step for the analysis was the creation of four additional variables taking advantage of the data were imputed: AR1, CA1, AR2 and CA2 (Table S1). The variables AR1 and AR2 represent the areas for the cross section of the rostrum at

0.5L and 0.25L. The value is given by convert the distances W (width) and D (depth) in the major 1/2W and 1/2D minor semi axes and apply the formula for calculate the ellipse area. When W and D have the same value we used the circumference formula to calculate the area. The variables CA1 and CA2 represent the left internal canal area at the distances of 0.5L and 0.25L respectively. The value is calculated in similar way that the variable AR using the variables N (width) and H (height) of the left canal but with the difference that 1/2H represents the major semi axis and 1/2N the minor semi axis when the ellipse formula is applied.

3.4 PCA with missing data for rostral variables

For the PCA analysis we excluded the specimen LACM 25491(Table S1) because has too much imputed data and only two values were real. Also the specimens LACM 25500 and LACM 25508 (Table S1) that appears to have no good identification were removed. We removed the variable DD1 because is lack for *K. audax* and the DVS distance because we consider it not real variable and is very similar to the VSPM distance (Fig. 4c). Prior to run the PCA, we applied a log transformation for data of 111 specimens distributed in 5 modern marlins species and two fossils specimens from Chagres Formation (Table S1). This PCA compared a total of 18 rostral variables.

3.5 PCA for articular variables

As we have few specimens with missing values for the articular bone we preferred debug specimens with missed values and the method used was the same used for the PCA for rostral variables. For articular, we analyzed 5 variables for 81 specimens distributed in 5 modern marlin species (Table S2) and one fossil specimen from Chagres Formation (STR1 31291) (Table S2).

CHAPTER FOUR

NEW TERMINOLOGY

4.1 New terminology implemented

Major differentiation of istiophorid fishes is based on the cross – sectional area of the rostrum, its length, shape and presence or absence of teeth (Nakamura 1985; Habegger 2014). Given its importance are used for species identification (Fierstine & Voight 1996) and based in our revision we decided introduce a new terminology to attend to standardize and facilitate the description of fossil species. The characters are the next: vertical alienation of the nutrient canals respect to the midline suture of the premaxillaries, lateral distribution of the canals in cross section and rotation of the left nutrient canal. The nutrient canals can change its vertical aligned respect to the midline suture formed by the premaxillaries (Fig. 7 a-c). They can be aligned in medial or central position (Fig. 7a), dorsally aligned (Fig. 7b) or ventrally aligned (Fig. 7c). The lateral distribution can be observed in three stages: centrally distributed where the canals are very close to the midline and the separation distance between both canals is not greater than the height of the canals (Fig. 7d); laterally distributed means that both canals are very distend each other and are more close to the outer margin of the premaxillar than the midline suture (Fig. 7e) and; intermediated distributed that means the canals are close to the midline but the separation distance between both is equivalent to the height of one canal or more but they never are more close to the outer margin than the midline suture (Fig. 7f). The last character for the canals is the rotation: dextrogyres when the left canal is rotated in clock-wise direction (Fig. 7g); canals are parallels when they are not rotated (Fig. 7h) and levogyres when the left canal is rotated counter clock – wise direction (Fig. 7i).

The rostrum shape and its distal tip also presents variations between istiophorids (Habbeger 2014) and we have been grouped the different shapes of the distal tips in three types: first is globular or bulled kind distal tip, this is a massive distal tip with a globular point, is observed in *Makaira* (Fig. 8a-b). Second form is slender or spear distal tip, is like the globular point but the difference is that is pointed and more stylized but not massive, is observed in *Istiompax*, *Kajikia* and *Tetrapturus* (Fig. 8c-d). Third form is depressed or plane distal tip, where the point is long and the most distal tip is more or less triangular in dorsal view as observed in *Istiophorus* (Fig. 8e-f) this is the most compact shape and also *Istiophorus* present the longest and most compact rostrum that represent one of the most specialized and optimized billfish weapons for prey capture (Davie 1990; Habegger 2014, 2015; Domenici *et al.* 2014; Stephano *et al.* 2015; Herbert – read *et al.* 2016; Kurvers *et al.* 2017)

4.2 Necessity of revision of istiophorid fossil species

Extinct species of istiophorid have been described from the late Eocene to Pleistocene with most of the descriptions based on isolated rostra (Fierstine 2006). To the date, there are 6 recognized fossil species of istiophorid fishes (Fierstine 2006) and four species have been described before of the first half of the XX century: *Istiophorus solidus*, *Makaira belgicus*, *Makaira teretirrostris* and *Makaira courcelli* (Rütimeyer 1857; Van Beneden 1871; Leriche 1926; Arambourg 1927) and two in recent times: *Makaira panamensis* and *Makaira purdyi* (Fierstine 1978, 1999b).

Although the number of the extinct species is limited to small number, there are some problems related with their taxonomy, especially species described in old papers. Authors do not agree with the locality and age of some of these types specimens (Schultz 1987; Fierstine 2006) and we attribute the problems to the next reasons:

(1) Type specimens deposited in Europe have not been revised after Schultz work (1987);

(2) Original publications are hard to get even in these days; specimens are not well-illustrated (Rütimeyer 1857; Van Beneden 1871; Leriche 1926; Arambourg 1927; Schultz 1987). In recent reviews of billfishes, some of these cryptic papers with key information do not appear in the bibliography or appears cited but is evident that original papers were not fully used (Schultz 1987; Fierstine1990, 2006); and

(3) the osteological material of modern istiophorids is few and is dispersed in many museums across the world. This makes complicated the study the fossil billfishes, but the situation changed after 1983 with the work of Izumi Nakamura that represent a very compressive study of istiophorids billfishes (Nakamura 1983) and when Harry Fierstine, interested in the study of fossil billfishes, created its personal osteological collection of istiophorid billfishes, a work made in the last 15 years. This collection represents the most complete in terms of number of species and specimens, that including sectioned rostrums. The collection is deposited in LACM today. Thanks to these important sources of information is possible to do better reviews and apply modern statistical analysis to study the morphology of fossil billfishes.

In this part of the thesis, we have revisited all 6 valid istiophorid species with help of all original literature that includes descriptions of the types species and direct review type specimens and osteological material from five different museums. We suggest some important changes in the taxonomy; and we solve all debates about type localities and ages for each species when is mentioned.

CHAPTER FIVE

SYSTEMATIC PALEONTOLOGY

Superclass: GNATHOSTOMATA Smith & Hall, 1990

Grade: TELEOSTOMI Nelson, 1994

Class: OSTEICHTHYES Rosen *et al.*, 1981

Order: ISTIOPHORIFORMES sensu Betancur-R *et al.,* 2013

Family: ISTIOPHORIDAE sensu Robins & De Sylva, 1960

Genus: *MAKAIRA* Lacépède, 1802

5.1 *Makaira*? sp. nov. 1

(Figs. 9-10a-b, 11-15; Tables 1-3, 5)

5.1.1 Specimen: STRI 31291 (Fig. 9) (the biggest and well preserved fossil billfish ever found), is a nearly complete skeleton which consists in 18 articulates and two fragmented and disarticulated vertebra in association with: nearly complete neurocranium and rostrum; left partial operculum; left and right suboperculums and supracleithrums; left epihyoid; partial lower jaw with predentary and partial right and left articulars; left partial pectoral girdle; disarticulated first left pectoral fin; articulated first anal fin, second dorsal fin, and caudal peduncle with multiple scattered radius. The CTPA paleontology group collected the specimens.

5.1.2 Type locality: *Makaira?* sp. nov. 1 was collected in Piña beach at the tide zone in the point: 9° 16' 5.99'' N, 80° 2' 51.46'' W over the burrows layer described by Coates (1999) (Fig. 2 - 3). Piña Beach is a rocky shore located on the coastline in the Piña Town, Chagres district, Costa Abajo Colón, Panamá (Fig. 1). The locality has 5.6 Ma (Messinian) (Collins *et al.* 1996) and crops out along prominent cliffs from the mouth of Piña river to ~3.6 km to SW of the town (Figs. 1, 3).

5.1.3 Taphonomy: the specimen is in great part articulated and preserves very fragile bones (Fig. 9). Its shows the lower jaw and two precaudal vertebrae displaced to the caudal zone (Fig. 9). The skull is compressed (Fig 11a-b) and the premaxillars are disarticulated of the prenasals and rotated about 45º (Fig. 11c) of the original position. The skeleton do not shows evidence of weathering by transport. Parts of the skeleton, which shows weathering, are only the bone exposed to tide conditions on field. In general the specimen shows low displacement and we suggest a rapid burial.

5.1.4 Diagnosis: medium size billfish (2.66 m), bill long (about 23.8% of the body length), slender and oval in cross section (0.5L and 0.25L) (Fig. 12). Two pair of large and oval nutrient canals higher than wide on the middle part of the rostrum in central position (Fig. 10 a-b). Denticles covering all dorsal surface of the bill (Fig. 12a) and the distal tip in ventral side (Fig. 12c). The rostrum is plane in its anterior part at the level of the VSPM distance (Figs. 11c, 12a). This surface is wrinkled where premaxillaries are divided but smooth where are fused. The plane zone forms a figure resembling a triangle on the ventral surface of the rostrum if is observed vertically (Fig. 11c, 12a) and looks slightly convex in transversal view at 0.5L (Fig. 10a). The cranium is wide and slightly stout (Figs. 11a-b, 12a), the vomer is moderate, oblanceolate, and has slight anterior projection (Fig. 11a-b). The condyles for the maxillaries are very close each of other (Fig. 11a-b). The socket in the articular has a very small medial process that is barely visible in dorsal view

(Fig. 13b). This socket is longitudinally elliptical, slightly apiculate ventrally and has square shape in lateral view (Fig. 13b). Has 13 caudal vertebrae (Fig. 9), the anterior vertebrae has well developed socket for ribs (Fig. 13a). The general shape of the vertebrae like hourglass shape, the centrum is strongly widened anteriorly and has high and wide square neural spines (Fig. 13d). Has moderate lateral process (Fig. 13d, g). The vertebra 22 and 23 are small and rectangular (Fig. 13h). The basal end of the first pectoral fin ray is nearly circular and the medial process is narrow and not pointed (Fig. 13c). The second dorsal fin has 7 frayed pterigiophores (Fig. 13e).

5.1.5 Description.

General features: STRI 31291 is a medium size and very well preserved articulated billfish whit an estimated total length of 2.66m (Fig. 9). Collected in two blocks that consists in: an articulated, compressed ventrodorsally partial neurocranium articulated with partial R. posttemporal, complete rostrum articulated with partial R. maxilla. The skull is preserved in ventral position and is associated with a vertebral column that consists in 18 articulated vertebrae and two disarticulated partials vertebra (Fig. 9). The vertebral column is associated with the second dorsal fin (Figs. 9, 13e), and articulated with the epurals 1 and 2 (Fig. 13h) of the caudal fin that, are associated whit ventral and dorsal lobe rays partially preserved. Scattered elements consists in preserved socket region of the L. partial operculum; L. and R. suboperculums and supracleithtums; L. epihyoid; articulated partial lower jaw; partial left pectoral girdle; disarticulated 1st. left pectoral fin ray an radials (Fig. 9) and articulated and partially preserved first anal fin (Fig. 13f). For a better comprention we have divided the description in five sections: rostrum, neurocranium, lower jaw, axial skeleton and appendicular skeleton.

Rostrum: The rostrum is complete and consists of the prenasals, premaxillary and nasals bones (Fig. 11c). Premaxillaries are disarticulated but are preserved over the prenasals and rotated 45º from its original position (Fig. 11c). The overall length and reconstruction of the rostrum (Fig. 12a) was estimated using CT scan. The estimated total length is 551 mm from its posterior edge of the nasal to the distal tip. The rostrum more or less plane dorsally and ventrally oblique and with an upward curve at its distal tip if is observed in lateral view. The distal tip shape is globular. The studied sections at 0.5L and 0.25L (Fig. 10a-b) were made in the exactly point that marks the half (0.5L = 275.5 mm) and one quarter (0.25L = 137.75 mm) of the total length of the rostrum using CT scan. The rostrum is oval in cross section (Fig. 10 a-b); the depth and width in each section is specified in the Table 1. Denticles are present and covers the complete surface dorsally and partially the ventral surface. In ventral view, the anterior part of the rostrum is plane from the point where premaxillaries are divided in two separated bones till 69.43 mm in distal direction (Figs. 11c, 12a). The surface of this zone is wrinkled where bones are divided but smooth and plane where are fused (Fig. 11c). This plane zone forms a figure resembling a triangle if is observed vertically (Fig. 12a). The ventral surface of the rostrum in transversal view at 0.5L is slightly convex ventrally but this convexity is caused by the plane surface described above (Fig. 10a). At the internal part in the proximal end of the rostrum, upon premaxillaries are fused prenasals. This fusion produces a protrude that continues in anterior direction. We conclude that this is an extension of the prenasals that are fused in the internally over premaxillaries at its proximal end (Fig. 11a-b). The plane structure at the proximal end of the rostrum in ventral view and the prenasals fused on the intern side of the premaxillaries could give a square and depressed shape of the skull (Fig. 12a). But nasals look unusually longer and stylize the shape of the rostrum (Fig 11c, 12a,d).

Each premaxilla is traversed by a large elliptical nutrient canals aligned and distributed centrally (Fig. 10a-b). The nutrient canals are medial aligned and centrally distributed. The canals are parallels and are not rotated as many other billfish species (Fig. 10a-b). The height (H1) and with (N1) of the canals are in the table 1. The ratio of H1/D1 is 0.25 indicating that nutrient canals are large (see table 2 for all ratios values). In modern species, large canals are only observed in *Istiophorus platypterus*. However in 28 reviewed specimens of *I. platypterus* any specimen has a nutrient canal with an H1 greater than 4.5 mm if this value is only compared with the 5.5 mm of the left nutrient canal observed in STRI 31291. In transversal section at 0.25L, medially and lying above the premaxillary canals is an obolanceolate foramina as is present in *Istiophorus platypterus* (Berry 1917) (Fig. 10b). This character could be indicative that the bones of the rostrum are not strongly fused (Schultz 1987) and not occurs in *Makaira* species. The comparative study of the ratios for the rostrum indicates that 7 o 9 studied ratios are in the range of *I. platypterus* and *M. indica* whereas 5 of 9 ratios are in the range of *M. nigricans* (Table 3). This information and the morphology allow us describe the rostrum as long, oval and slender in cross section.

Neurocranium: The neurocranium is incomplete. The left half part of the skull and some bones of the ventral part as basioccipital, intercalars, prootic and basisphenoid are poorly preserved (Figs. 11a-b). Radios between cranial measures (PTW/CAL and ACW/CAL) are 0.64 and 0.32. These two ratios indicate that the cranium is wide and slightly stout (Nakamura 1983) (Fig. 12a,d). The studied relation between length and height of the cranium for 7 istiophorid billfishes indicates that these ratios belong to a square shape characteristic of *Makaira* and *Istiompax* species and its measured values are more close to *Is. indica* than *Makaira* (Nakamura 1983).

The parasphenoid is broken in two pieces, one is fused with the vomer and the other one is articulated with the neurocranium (Fig. 11a - b). The preservation of the parasphenoid is very bad for calculate ratios with this bone. The vomer is slightly displaced to the left and has suffered damage during the filed collection (Fig. 11a-b). Vomer is the massive bone that articulates posteriorly with the parasphenoid, laterally with the lateral ethmoid, dorsally with the ethmoid and anteriorly by two large condyles where is placed the maxilla (Fierstine 1978). The condylar surface of the vomer that articulates with the maxilla is nearly round and without flat facets that face anterolaterally (Fig. 12a). Measures of the vomer are: width: 34.81 mm and length: 107.3 mm. The bone has a slight anterior projection of 3.71 mm between the condyles. Fierstine (1978) indicated that this anterior projection might be variable because a large *M. nigricans* lacks such a structure whereas two small *M. nigricans* has slights projections. The general shape of the vomer is oblanceolate (Figs. 11a - b, 12d), looks less massive that vomer in *Makaira* and *Istiompax* species. Based on the observed measured we can define this vomer as moderate as occurs in *Istiophorus* and *Kajikia* but different to the wide vomer of *M. nigricans* and *Is. indica* and to the narrow vomer of *Tetrapturus* (Nakamura 1983). In general way the vomer is very similar in shape to *I. platypterus*, however has slight anterior projection and the condyles for the maxillaries are very close each of other with only 11.51 mm of separation, this character only observed in this species.

Lower jaw: The lower jaw is formed by the predentary and the paired bones: dentary and articular (Davie 1990). All bones of the lower jaw in the specimen STRI 31291 are present but dentaries are poorly preserved (Fig. 9). The lower jaw is articulated and is displaced into the second block (Fig. 9a, c). The left articular is disarticulated and is located in the first block where are the pectoral fin rays (Fig 9a - b). The predentary is fine and has the shape of isosceles triangle. The tree studied ratios (PW/PL, PD/PL and PD/PW) (Table 2) of the predentary match with the ranges observed in *I. platypterus, M. nigricans and I. indica.* However, Fierstine (2001) after study 52 predentaries from Lee Creek Mine indicates that the predentary not provide strong information to determine billfishes to species level. Nevertheless the thin and light shape of this predentary is more similar to *Istiophorus* than *Makaira* species.

The dentaries are very poorly preserved. The entire ventral surface is damage and missed and only is preserved the dorsal surface as a thin line to the distal part of the bone. (Fig. 9a, c) However, was possible to estimate the distance DJL using as reference the mandibular foramens. At the same way, the DAD distance was estimated using the PD value in the predentary as reference. The estimated ratio between DAD/DJL is 0.40 indicating that is similar to *I. platypterus* and not is tall and strong denary as *Makaira* and *Istiompax* (Fig. 15, Table 2) (Fierstine 2001). Both articulars are very good preserved. Of five ratios analyzed for the left articular, two (ATW/Al and AW/ATW) has fallen out of the observed values for 8 billfish species (Table 2, 3). Comparing all ratios (Fig. 14b) and doing observations we can conclude that the socket of this articular has an unusual shape

(Fig. 13b). The ratio of ATW/AL is 0.83. This value is the most small observed compared with all other modern billfish species (Table 2). This is caused for the very small medial process that is barely visible in dorsal view (Fig. 13b). The ratio between AW/ATW is 1.10 and is the greater observed value when is compared with other modern billfishes (Table 2). This means that the distance AW (18.76 mm) is greater than the ATW (17.08 mm) distance. These values also are not observed in any modern and fossil istiophorid billfish. This combination of ratios values and the very small medial process gives to the socket, a longitudinally elliptical shape in dorsal view, that is slightly apiculate in its inferior part and square shape in lateral view (Fig. 13b). This unique shape for the socket also is showed in the result of the PCA analysis (Fig. 14b) that corroborates our description.

Axial skeleton: the vertebral column is nearly complete and consists in 20 preserved vertebrae: 5 precaudals centra articulated (+ two incomplete and disarticulated precaudal centra located in second block) and 13 caudal centra (Fig. 9). In modern species only the genus *Makaira* and *Instiompax* has 13 caudal vertebrae while *Istiophorus* and *Tetrapturus* has 12 caudal vertebrae (Nakamura 1983, 1985; Davie 1990). We assumed that the specimen had 24 vertebrae as all modern istiophorids and only that four precaudal vertebrae are not preserved. The first vertebra is partially preserved over the second block and is recognizable by the cay that articulate with the exoccipital bones (Fig. 9a, c). The other disarticulated vertebrae (Fig. 9a,c) could belong to the position number three by having greatly hypertrophied anterior zygapophyses (Gudger 1940). An anterior vertebra has well-developed socket for the ribs in the centrum as occurs in the genus *Makaira* and *Instiompax* (Fig. 13a) (Davie 1990). In general way, vertebrae has hourglass shape (Fig. 13) (Nakamura 1985; Davie 1990). The centrum is strongly widened anteriorly and a well-developed lateral process is visible between vertebrae 12-14 (Fig. 13d, g). The lateral process is only present in the modern marlins *M. nigricans* and *I. indica* on the ninth or tenth to nineteenth or twentieth vertebrae (Nakamura 1983, 1985, Davie 1990). The relation of the ratios of NH/CL (0.99) and NL/CL (0.96) for the vertebra 14 match with vertebrae of *Makaira* and *Istiompax* indicating a high and wide, square neural spines (Fig. 13d) different to the triangular spine of *Istiophorus* and the rectangular or trapezoid shapes of the spines observed in *Tetrapturus* (Nakamura 1983, 1985) (Fig. 5e).

Of eight characters for the vertebrae 22 and 23 only four were studied (Table 1). The hypural plate (vertebra 24) is to damage and is impossible to study directly. Following the Fierstine methodology (2001) whit the available characters only were possible to study the ratio of VPD/CL for both vertebrae. The ratio VPD/CL of the vertebra 22 fell out of the observed range for eight extant billfish species whit a very low value (0.30) (Fig. 15, Table 2-3). This could be interpreted as a short dorsoventral diameter combined with a large vertebral length that gives a rectangular shape to the vertebra like *Tetrapturus* species. The VPD/CL for the vertebrae 23 is also low (0.43) but corresponds only with the observed ratio for *I. platypterus* (Table 3). However the CL for this vertebra has been estimated because the vertebra has several damage in its posterior part (Fig. 13h). As the vertebrae 22, 23 and 24 that forms the caudal peduncle compounds an unique form in each species of billfish, based on the morphology of the vertebra 22 and 23, we can conclude that the vertebrae of the caudal peduncle in this fish have a more rectangular shape than other knows marlins (Fig. 13h).

Appendicular skeleton: the appendicular skeleton are the bones of the appendages that includes paired and unpaired fins (described above) (Davie 1990). The left pectoral girdle is partially preserved in medial view (Fig. 9a-b). The scapula is completely missed. The anterior dorsal process of the cleithrum is damaged and the coracoid is nearly complete except the zone that articulate with the scapula (Fig. 9a-b). The bad stage of preservation of the pectoral girdle makes impossible compare with other istiophorid billfishes but based on the morphology of the first left pectoral fin ray (= marginal ray) and the size of the pectoral girdle we can assume the articular surface on the dorsal edge of the scapula is markedly convex and curves smoothly from the lateral to medial surface of the bones (Morrow & Posner 1957; Wapenaar & Talbot 1964). The basal end of the first pectoral fin ray is enlarged and nearly its dorsal portion (Fig. 13c). This form makes not possible confuse it with the plane articulation of *I. indica*. Compared with *Istiophorus* and *Makaira* – *Istiompax* species, the ratio value between FAW/FW match with the ratios range of *I. platypetrus* and *M. nigricans* but differs of the values for the ratios observed in *I. indica* (Table 2, 3). With our direct comparison of the basal end of the first pectoral fin ray of the specimen STRI 31291 with *M. nigricans* and *I. platypterus* we concluded that is more round and the median posterior process is narrow and not pointed that the mentioned species (Fig. 13c) (Morrow & Posner 1957).

The second dorsal fin is articulated and very well preserved and consists in 7 pterygiophores and 5 articulated frayed spines (Fig. 13e). According with the numbers of pterygiophores we assume that STRI 31291 has 7 frayed spines on the second dorsal fin. The numbers of frayed spines on the second dorsal only are out of the range for the modern billfishes *T. albidus* and *T. audax* that has a maximum of 6 spines (Nakamura 1985). The first anal fin is also articulated, well preserved but is flipped and rotated about 50º from its original position (Fig. 13f). For this fin are 9 preserved pterygiophores and five spines. The first spine is missed and are preserved the spines 2, 3, 4, 9 and 10 (Fig. 13f). This fin is incomplete and the preservation state not allows comparing it with other species. There are several rays of the first dorsal fin preserved over the first block and only one radius preserved over the second block (Fig. 9a, c). We can infer the presence of a large first dorsal fin as all modern marlin species but there is not enough evidence of the presence of a huge first dorsal fin as occurred in *I. platypterus*.

5. 2. *Makaira?* sp. nov. 2

Figs. 10,14a, 15-16, Tables 1-2, 5.

5.2.1 Referred specimen: STRI 31293 is a nearly complete rostrum.

5.2.2 Type locality: the specimen was collected in Piña beach at the tide zone (Fig. 3) about 20 meters western from where was collected the specimen STRI 31293 at the point 9° 9' 16'' N; 80° 2' 71'' W. The fossil were collected in an eroded rock that belong stratigraphically to a layer placed approximately 5 m over the layer where was collected the first specimen.

5.2.3 Taphonomy: The specimen was inside of eroded rock and given by the environmental conditions the matrix was oxide and the specimen surface is bad preserved. Surface is worn (Fig. 16) and is not possible to see alveoli for denticles in any part of the rostrum. However all other characters are well observed. The specimen has associated lower jaw (Fig. 16d-f) that was contained in the block from where the rostrum was extracted.

5.2.4 Diagnosis: rostrum is slender (spear – kind shape), the VSPM distance is about 30% of the rostrum length. This means that the point where the premaxillary begins to divide in two separate bones includes more or less 60% of the total rostrum length. Rostrum is round at the 0.25L cross – section (Fig. 10b-c) and, at this level the premaxillaries are separated. Nutrient canals are rounds in both cross - sections, its position respect to the mean line suture o is ventral and the distribution is central (Fig. 10b-c).

5.2.5 Description.

The rostrum is nearly complete and consists in prenasal, premaxillary and complete left nasal (Fig. 16a-c). The overall length is 611 mm and approximately 13 mm were missing of the distal tip. We estimated a total bill length of 624 mm. The rostrum is stout, oval at 0.5L (measured at 307 mm from the tip) and nearly round at 0.25L (measured at 155 mm from the tip, see the out range ratio D2/W2 on the Table 2) (Fig. 10c - d). The distal tip is very acute and compressed. The premaxillaries begins to be separates at 248 mm from the distal tip (VSPM). This distance is approximately 60 % of the total length of the rostrum and the division is visible in cross section at 0.5L distance (Fig. 10c). The nutrient canals are located slightly ventral to the center, are large and nearly rounds (Table 1, Fig. 10c-d). These characteristics make different STRI 31293 to the oval canals observed in all others istiophorids and remember the oval canals of *M. panamensis* (the largest observed: H1= 8.5mm and N1 = 5.0 mm) for a specimen with an estimated rostrum length of 953 mm (Fierstine 1972). The surface of the specimen is bad preserved and is not possible see denticles or alveoli but is expected its presence. The rostrum is compared with other specimens in assumption that the posterior edge of the left nasal is the same transverse plane as the lateral ethmoid in more complete specimens (Fig 16a) (Fierstine 1999a). The lower jaw is preserved and is represented by partial right and left dentaries (Fig. 16d-f). The ratio of the dentaries (DAD/DJL) is on the range of *Istiophorus* and *Kajikia* but not in genus *Makaira* (Fig. 15, Table 2). This means that the length measured from the mandibular foramen to the anteriormost denticles is practically in proportion gives a rectangular shape more than square shape observed in *Makaira* and *Istiompax* (Fig. 15). The DJL distance in *Makaira* species is larger for a stronger joint between dentaries but in the specimen STRI 31293 looks small. According with this is expected that the mandible have reduced bite force (Habegger 2014). Of 10 ratios studied for this specimen, 5 are in the range of *I. platypterus* and *M. nigricans* while four are in the range of *Is. indica* (Table 4). This discordancy and one ratio out of range difficult take a decision to determinate this specimen. We could either determinate the specimen STRI 31293 as new *Makaira* or *Istiompax* species. According with the PCA analysis for the rostrum variables we can observe that STRI 31293 is closer with *Makaira* and *Istionpax* but not grouped also is very distant of *Istiophorus*. This specimen also represents an individual with characters values out of all observed ranges for modern marlins species (Fig. 14).

5.3 Comparison of new species with other istiophorid fossil forms

Makaira? sp. nov. 1 is different to *M. belgicus* by having centrally aligned and distributed nutrient canals. These canals are big, ovals higher than wide and located in parallel position. This is different to the dorsally aligned nutrient canals in *M. belgicus* (Fig. 7b). Is different to unmanned gen. nov. *M. courceli* because *Makaira*? sp. nov. 1 has a generalized oval shape in all length of the rostrum, does not have the obtuse angle in the first half of the rostrum neither additional par of nutrient canals on the distal end (Arambourg 1927). It is different to the massive, big and stout rostrum of *M. panamensis*, especially by having round shape in 0.5L and 0.25L distances. Also *M. panamensis* has central aligned canals, but slightly displaced in ventral direction (Fierstine 1978). *Makaira*? sp. nov. 1 cannot be confused with *M. purdyi* because this species consists in a very different short and stout rostrum of a big size fish (Fierstine 199b).

Our PCA analysis shows that the rostrum of *Makaira*? sp. nov. 1 is and *Makaira* sp. nov. 2 are out of group for all modern Istiophorid species (Fig. 14a) while its mandibles are in the range for *Istiophorus* and *Kajikia*. That means these species have rostrums more related to big size marlins but also a reduced bite force in comparison with *Makaira* and *Instiompax* (Habegger 2014). But in the PCA for rostral variables they are located very distant of the *Istiophorus* – *Kajikia* group. This means that we also cannot include this species in these two genera because our analysis for a combination of rostral variables group Chagres species out of these groups (Fig. 21a). *Makaira*? nov. sp. 1 also cannot be included in the genus *Tetrapturus* because the body size is out of the range for the spearfishes. We have propose locate both species in a new genera but before perform a phylogenetic analysis is not possible corroborate it.

5.4 *Makaira belgicus* (Leriche, 1926)

Figures 17b, 18f, Table 5.

The specimen (IRSNB P1117, middle Miocene, Anvers, Belgium) is the oldest known species of the genus *Makaira* and is represented by a 200 mm distal rostral fragment. Fierstine (2006) argued that *M. belgicus* comes from the Pliocene of southern France, but Shultz (1987) attributed it to the age of Middle Miocene. The holotype of *M. belgicus* was originally published as paratype of *M. teretirostris* (Rütimeyer 1857) in a paper, which described by second time this species *M. teretirostirs* (Van Beneden, 1871). However a later research indicated that these two specimens were different species and the age and type locality of *M. belgicus* was corroborated (Leriche 1926).

The rostrum is slender in shape including the distal tip and oval in cross section (Fig. 18f). Has a round and small pair of nutrient canals in dorsal position, centrally distributed in parallel position (Fig. 18f). Prenasals are represented by grooves (Fig. 17b) (Leriche 1926; Shultz 1987). This shape of the distal tip is different to the globular bullet-type distal tip of *Makaira nigricans*. The alveoli for denticles are present in all ventral, and dorsal surfaces with exception of the sutural zones for the prenasals bones (Fig. 9b). The ratios for the 0.5L fall within the rage of values for the recent *M. nigricans* and fossils *M. nigricans* of Lee Creek Mine but its nutrient canals are dorsally aligned and centrally distributed in cross section representing this a unique combination not observed in any other istiphorid (Fierstine 2001).

5.5 *Makaira purdyi* Fierstine, 1999b

Figures 17c, 18g, Table 5.

The specimen (USNM 481933, early Pliocene, North Carolina) is an unusual 480 mm short and stout bill (Fig. 17c) that is nearly round in cross section with a globular distal tip (Fig. 18g). The most diagnostic characteristic is that prenasals terminate close to the distal tip. The rostrum massive and is morphologically distinct from any Recent or fossil istiophorid by short and stout fused portion of premaxillae with denticles covering at least one half of its dorsal surface (Fig. 17c). The nutrient canals are ovals and levogyres, are ventrally aligned and centrally distributed at the 0.25L distance (Fig. 17c).

5.6 *Makaira panamensis* Fierstine, 1978

Figures 18h, 19, Table 5.

The specimen (USNM 18710, holotype, Late Miocene, Chagres sandstone, Caribbean coast of Panamá) is a large neurocranium with a poorly preserved rostrum with and estimated length of 953 mm (Fig 19a-c). The specimen is similar to *M. nigricans* and *M. indica*. However, it differs from both species by having the largest nutrient canals observed (height 8.5 mm and with 5 mm measured at 560 mm from the orbit, are medially aligned and centrally distributed (Fig. 18h). In dorsal view has a nasal cavity divided in two by a partition (Fig. 18h). The rostrum is oval apparently in all its length but its preservation state made difficult recognizes if is round, or oval at 0.25L. *M. panamensis* differs from modern marlins by having a triangular basioccipital process (Fig. 19d) rather than an elongate. By having a massive and have probably more elongate orbit as well a more depressed skull (Fig. 19) (Fierstine 1978).

5.7 *Makaira nigricans* Lacepède, 1802

Figure 20, Table 5.

This species was misidentified like *Makaira teretirostris* (Rütimeyer, 1857) (Pliocene of Montpellier, France) is a large 520 mm rostrum originally described as cetacean of the genus *Encheiziphius* (Rütimeyer 1857). Its redescription in the genus *Brachyrhynchus* was based in a cast and scale illustration made under supervision of L. Rütimeyer (Van Beneden 1871; Van Beneden & Gervais 1880). The original specimen is missed, but may be housed in in some of the museums in Basel (Switzerland), Montpellier, or Paris (France). Works about the fossil vertebrates from the Pliocene sandstone of Montpellier can help to find the location of this collection (Roman 1922). Here, we made a careful review of the original illustration (Fig. 20) and compared its measurements with the measures published in the original paper (Rütimeyer 1857). We found that this illustration was done in a perfect scale and the plate includes seven schematic diagrams of cross sections (Fig. 20) in well details that never have been mentioned in others papers (Van Beneden 1871).

The rostrum is large, stout, with oval shape in cross section at 0.5L and becomes more width as we look toward to the 0.25L distance and distal tip (Fig. 20). The distal tip is almost round in its base and becomes oval in the middle part and finishes in a round tip (Fig. 20). This gives to the distal tip a globular – type shape, as has *Makaira nigricans*. There are two oval nutrient canals centrally aligned and distributed (Fig. 20h). *M. teretirostris* was synonymized with *M. belgicus* by Shultz (1987). On the other hand, later works show that ratios of *M. teretirostris* are slightly outside of the ranges of modern *M. nigricans,* but are within range of *M.* cf. *M. nigricans* from the Early Pliocene of Lee Creek Mine

(Fierstine 2001, 2006). Based on this information and location of nutrient canals in *M. belgicus*, we concluded that the species is not junior synonym of the *M. teretirostris*. Furthermore, there are some deviations of the measures on these works that we assign to less accurate methods. For example data taken from the cast (L = 522mm, W1 =52 mm) (Van Beneden 1871) not coincides with the data published in the original description (L = 530 mm, 58 mm and 50 mm in the wider and narrower parts of the transversal section in the base) (Rütimeyer 1857). We also confirmed these measures in the illustration (Fig. 20). Consequently, based in our analysis we conclude that *M. teretirostris* is synonym of *Makaira nigricans*.

5.8 Unnamed gen. nov.

Type species: *Makaira courcelli* (Arambourg, 1927)

Figures: 17a, 18a-e, Table 5.

A slender rostrum represents the specimen with a general oval shape in cross-section that terminates also in a slender and pointed distal tip (Fig. 17a). The more remarkable features are the angularly obtuse rostrum in the ventral surface (Fig. 18a-b) and the presence of two additional small vestigial nutrient canals (Fig. 18c-e). These additional canals are located in dorsal position and aligned laterally but are present only on the distal end of the rostrum. I propose to transfer *M. courcelli* to a new genera after review all modern and fossil Istiophorids species and for make emphasis in this important characters.

Istiophoridae gen. nov. *courcelli* (Arambourg 1927) (MNHNP 250 Late Miocene, Algeria) is a species collected in "Les Planteurs" locality from the pre – evaporites period of Tripoli Unit which has Messinan age (Landini & Menesini

1984, Carnevalle 2002; Gaudant 2008). The material attributed to the species consists of two rostrums and one predentary. The description here is based in the specimen (ORA 1778) illustrated by Arambourg (1927) and the associated predentary (ORA 1781). The second rostrum is very fragmented and its shape is depressed and never has been sectioned. This condition and its shape make us believe that this rostrum (ORA 1780) is not an istiophorid and will be described and studied later (out of the thesis).

The rostrum is 295 mm long and present many fractures. It is rather slender and its dorso-ventral general shape is more or less elliptical (wider than height) (Fig. 17a). In lateral view is straight dorsally and slightly curved upwards ventrally (Fig. 17a). The grooves on the dorsal surface of the specimen are interpreted to be areas for articulation with prenasals. The rostrum is covered by conical denticles that are restricted to the ventral and lateral surface of the specimen. The denticles located in the lateral surfaces are the bigger. The rostrum has two continuous nutrient canals in cross section. Here we describe six transversal sections illustrated by Arambourg (1927) because the rostrum is very variable in deterrents cross sections: the first (1) is represented by the fracture at the proximal end of the rostrum that is the cross section at the 0.5L distance (Fig. 18a). At this distance the rostrum is oval in cross section but angularly obtuse in the ventral surface. This gives a convex shape down the rostrum but this convexity decreases gradually (2) (Fig. 18b) up to approximately 139 mm (3) measured from the proximal end (Fig. 18c). At this distance the rostrum is oval in cross section and appears two smaller canals located superiorly of the first pair but are further away from the midline suture. These small canals are visible by a distance of 62 mm until the transversal section located at 200 mm (4) from the proximal end and gradually disappears (Fig. 18d). The transversal section at 200 mm (Fig. 18d) is also oval but plane in its ventral surface. This plane surface is extended from this distance by 46mm where the rostrum acquires oval shape again. Finally the section at 260 mm (5) (Fig. 18e) and 290 mm shows a reduction of the lateral sides that gives a needle shaped distal tip (Fig. 17a). Istiophoridae nov. gen. *courcelli* has all features of istiophorid fish but the additional pair of small canals (possibly non functional because are not continuous in whole length) are typical characteristics of primitive billfish families (Fierstine 2006). This character has probably plesiomorphic character and it is shared by new unnamed genus with family Paleorhynchidae (Fierstine 2006). On the other hand, the significance of this (partly confusing) character in not fully understood for the moment. Anyhow, the Messinian age of this specimen makes no possibility of any confusion with Paleorhynchidae or Xiphiorhynchinae (Xiphiidae) and makes an interesting link between the family Istiophoridae and extinct billfish families.

XIPHIDAE Swaison, 1839

Xiphiorhynchinae Regan, 1909

Xiphiorhynchus van Beneden, 1871

5.9 Xiphiorhynchus solidus Van Beneden, 1871

Figures 18i, 21, Table 5.

Originally described as *Brachyrhynchus solidus* Van Beneden 1871, was renamed as *Istiophorus solidus* following the tradition of early workers to place fossil billfishes with disparate morphology in *Istiophorus* (Fierstine 1978, 2001b). Later was placed in *Xiphiorhynchus* (Xiphiidae: Xiphiorhynchinae) by lack of central canal and presence of prenasal bones (Shultz 1987) and synonymized with *Xiphiorhynchus priscus* (Agassiz, 1839 – 44). After this was relocated again in Istiophoridae by having groves for prenasal bones and two nutrient canals but renamed as "*Istiophorus*" *solidus* to recognize its importance without establishing a new genus (Fierstine 2001b, 2006). A review several fossil and modern specimens and considering the Late Eocene age of "*Istiophorus*" *solidus* and type locality in Belgium (Genth), where also had been recovered *Xiphiorhynchus elegans* of the Eocene age (Woodward 1901). We consider that "*Istiophorus*" *solidus* (Van Beneden, 1871) is not an istiophorid and recommend located it in the genus *Xiphiorhynchus* in agreement with Shultz (1987). However, *X. solidus* is not synonym of *X. priscus*. A synonymisation between *X. solidus* and *X. priscus* is not possible because *X. priscus* consists in a nearly complete skull and only the posterior part of the rostrum is preserved (Agassiz 1839 - 44), while *X. solidus* is represented by anterior end of the rostrum. This condition and the poor preservation state of *X. solidus* makes impossible establish a good relationship between these two specimens, and consequently both taxa. Until new evidence is recovered we recommend not synonymize and maintain the species in the genus *Xiphiorhynchus*.

The specimen (IRSNB P643, late Eocene, Ghent, Belgium) is a distal 130 mm rostral fragment, oval and strongly depressed (Fig. 21). The specimen has a pair of groves that runs almost all the length of the dorsal surface (Fig. 21a-b). According this condition we inferred that its distal tip finish in flat compressed tip. Rostrum is hard and is composed by fibrillar bone (Fig. 21); there are not alveoli for denticles in any part of it (its absence could be related with state of preservation). In cross section not midline suture is observed. Also, has a pair of large and round nutrient canals that are aligned medially and laterally distributed (Fig 18i, 21d-e). A study using radiographies shows that these two channels run all the distance in the internal part of the specimen (Shultz 1987). In cross section, is visible a structure that appears to be a third canal filled with plaster dorsally aligned and in central position (Fig. 21d) that could be secondarily added during the original preparation. The X- ray observation also suggests the possibility that this represent a third canal located in central position over the two lateral canals (Fig. 18i) (Shultz 1987).

CHAPTER SIX

ISTIOPHORID BILLFISH EVOLUTION

6.1 Relationships between fossil billfishes and other groups

The phylogenetic relationships of billfishes have been explored in numerous morphological and molecular studies with resulting phylogenetic hypotheses differing dramatically (Finnerty & Block 1995; Orrell *et al.* 2006; Collette *et al.* 2006; Little *et al.* 2010). Have been wide accepted that billfishes belongs to Scombroidei based in strong support of morphological data and some authors have classified billfishes in the suborder, Xiphioidei (Johnson 1986; Finnerty & Block 1995; Orrell *et al.* 2006; Collete *et al.* 1984, 2006). More recent results suggest a close relationship between billfishes (Istiophoridae and Xiphiidae) and barracudas (Sphyraenidae) and classified this group in the order Istiophoriformes (Miya *et al.* 2013; Nelson *et al.* 2016). This hypothesis also considers the fossil billfish families Hemingwayidae, Blochidae and Paleorhynchidae (Fierstine 2006; Nelson *et al.* 2016). An alternative hypothesis based in mitochondrial and nuclear DNA indicates that billfishes are more related to flatfishes (Pleoronectiformes) and jacks (Carangidae) with a common billfish/ flatfish /jack ancestor (Little *et al.* 2010). A general vision considering that the oldest billfish record is from Late Paleocene (Fierstine 2006) makes us to accept the classification of billfishes in the order Istiophoriformes (Nelson *et al.* 2016). Istiophoriformes includes four extinct billfishes families according with recent studies (Monsh & Bannikov 2012) and two extant families (Istiophoridae and Xiphiidae) (Nelson *et al.* 2016). Morphological evidence suggest Xiphiidae as the sister group of Xiphiorhynchidae and that these two families are closed related with Blochidae (Fierstine & Monsch 2002; Monsch & Bannikov 2012). Whereas Hemingwayidae is sister group of Istiophoridae and are associated by the extreme synapomorphy of foliarly shaped neural and haemal speines (Sytchevskaya & Prokofiev 2002; Monsch & Bannikov 2012). The family Palaeorhynchidae with *Aglyptorhynchus* from the Early Paleocene appears to be the most primitive billfish family (Monsch & Bannikov 2012). But Heingwayidae with its monotypic species *Hemingwaya sarrisa* from Late Paleocene of Turkmenistan is the oldest fossil record of billfish (Fierstine 2006). The oldest billfish *Hemingwaya sarissa* is a high-specialized fish by having elongated upper and lower jaws in equal size with multiple rows of villiform teeth, the hemal and neural spines widened and leaf shaped like istiophorids but caudal skeleton builded as Scombrini (Monsch & Bannikov 2012). Families Hemingwayidae and the close relative of crown billfishes, Sphyraenidae have the oldest fossil record from the Late Paleocene (Fierstine 2006; Santini *et al.* 2015) and the oldest Scombridae dates from the same age interval period (Patterson 1993; Monsch 2005, 2006). While Carangidae has estimated stem age from Cenomanian and the oldest fossil is from the Early Paleocene from Monte Bolca (Santini & Carnevale 2013). Additionally flatfishes appear for first time in the Early Eocene with forms that exhibit incomplete eye migration (Friedman 2008). We suppose that the study of extinct billfishes families and primitive Scombridae and Carangidae can help to understand the billfish's origin. The Paleocene – Eocene is an interval for rapid diversification occurred in the pelagic fish community following the K-T extinction (Guinot & Cavin 2016; Sibert & Norris 2015) and me exploration in Paleocene deposits or go back in time to the Cretaceous can help to understand the evolution of billfishes and find a common antecessor.

6.2 Istiophorid billfish adaptations

The oldest record for istiophorid billfish is *Makaira belgicus* from the Middle Miocene of Ambers Belgium. Independent of the origin, after our extensive review of literature and osteological material, we can infer that istiophorid billfish evolution was a process that evolved several morphological changes. These changes are related to high-speed displacement in open ocean environment and capture preys in high velocity with specialized weapon (Davie 1990, Hebranck *et al.* 1990, Domenici *et al.* 2014; Stephano et al. 2015). The bill is formed by the loss of mandibles of equal length and elongation of the upper jaw (Fierstine 2006; Habegger 2014) Major changes are size and weight increment (Santini & Sorenson 2013), increase of the eye orbital size (Davie 1990; Fritsches *et al.* 2000) reduction of the inferior mandible (Fierstine 2006; Habegger 2014), enlargement and optimization of the superior mandible to form strong and specialized structure to impale preys (Fierstine 2006, Habegger 2014, 2015; Domenici *et al.* 2014), high ossification of the skull (Davie 1990), reduction of number of vertebrae to 24 that are interlocked by the haemal and neural prezygapophysis (Gregory & Conrad 1937; Davie 1990; Fierstine 2006) and high modified caudal peduncle (Davie 1990; Hebranck *et al.* 1990). Physiological adaptations of billfish include endodermy by having a heather organ beneath the brain that serves to warm the brain and the eyes 4ºC above the water temperature (Carey 1982; Davie 1990; Block & Finnerty 1994). Also istiophorid can rotate the eyeball in all directions in its orbits and this adaptation is related to visual stabilization to follow preys in high-speed movements and the heat organ is related to improve information processing in the visual system (Davie 1990).

6.3 Chagres Formation fossil marlins

Makaira? sp. nov. 1 from the Late Miocene from Chagres Formation, Panama shows an interesting combination of characters in the skull and caudal skeleton bones. These features are wide skull as occurs in *Makaira* and *Istiompax* (Nakamura 1983) combined with a rostrum that have a globular distal tip and general shape as *Makaira* but is more slender (See Habegger 2014). These differences are not obvious visually and are represented in our PCA analysis for rostral variables (Fig. 14a). The internal canals are big and more height than wide (Fig. 10a-b). Generally big canals are observed in fossil istiophorids with the exception of *Istiophorus platypterus* that is the only modern species that exhibit big nutrient canals (Fierstine 1978, 1998, 1999, 2008; Schultz 1987; Carnevale *et al.* 2002). Moderate wide vomer in *Makaira?* sp. nov. 1 (Fig. 12c) is similar in shape as occurs in *Istiophorus* and *Kajikia* (Nakamura 1985) and have as distinctive feature that the anterior condyles for articulate the maxillars are very close each other (Fig. 11a-b, 12a,c). In modern billfishes a wide and highly ossified skull is related with a stout massive rostrum and with wide vomer (Nakamura 1985, Habbeger 2014). But a wide skull in *Makaira*? sp. nov. 1 is related with moderate vomer (Fig. 12c). This pattern is unique for this species and is not observed in extant istiophorids cause wide vomer is associated with wide and highly ossified skull and moderate vomer with more narrow skulls that shows losing of mineralization (Nakamura 1983; Habegger 2014). *Makaira?* sp. nov. 1 in the anterior part of the dentaries where is the interdentary joint area present ratios more related to *Istiophorus* and *Kajikia* (Fig. 15). This means that the shape is longer than square in the anterior part of dentary as occurs *Makaira* and *Istiompax*. The socket region for the articular also have a very small medial process that is barely visible in dorsal view (Fig. 13b). This socket has unique shape between marlins and is more related in to biggest species than smallest (Fig. 14b). The reduction of the process (that is well visible in biggest species of billfishes) is related to fewer surfaces to connect the adductor muscles meaning musculature reduction (Davie 1990). This feature suggests that bite force is not important for *Makaira?* sp. nov. 1. Biomechanical studies, indicates that biggest marlins have bigger anterior and biggest absolute bite force while smaller marlins species have smaller anterior and smaller absolute bite force (Habegger 2014). The mandible of *Makaira* sp. nov. 2 (Fig. 15) also show this same pattern. However its rostrum is biggest than *Makaira?* sp. nov. 1. and both rostrums, are not so long as modern *Istiophorus* and *Kajikia*. Additionally the Chagres sandstone includes *Makaira panamensis* that had a wide and highly mineralized skull with stout rostrum (Fierstine 1978; Fierstine 2006). *Makaira panamensis* is a big size marlin and tits wide and large vomer is consistent with all other features of the skull and rostrum as occurs in modern big size marlins (Fierstine 1978; Nakamura 1986). The fossil record of istiophorids suggest that oldest istioporids belong to *Makaira* and dates from the Late Miocene (Leriche 1926; Fierstine 1978, 1998, 1999, 2001, 2008; Carnevale *et al.* 2012). From the Late Miocene of Algeria also is *Makaira* gen. nov. *courcelli* (Arambourg, 1927) that shows very distinctive rostral shape and cross section anatomy with features that could be primitive characters (Figs. 17a, 18a-e). This species was described with two rostrums but our revision indicates that the second specimen could belong to the genus *Xiphiorhynchus* and could close the 10Ma gap that is between the first apparition of Xiphiidae and last apparition of

Xiphiorhynchus connecting the billfish fossil record (Fierstine 2006). Other species as *M. purdyi*, *I. playpterus*, *Is. indica* and *K. albida* appears in the record fossil during the Early Pliocene of Yorktown Formation in North Carolina (Fierstine 2001, 2006; Santini & Sorenson 2013). While Spearfishes (*Tetrapturus)* have no fossils record to the date (Fierstine 2006) and appear to be the most diverged istiophorid (Santini & Sorenson 2013). Molecular evidence suggest Cretaceous origin for billfishes with a radiation of extant istiophorid starting during the Early Miocene (~19Ma) and most species having split from their closed relative since the beginning of the Pliocene (~5Ma) (Santini & Sorenson 2013). Due to the istiophorid fossil record is mostly fragmented and sparse the excellent preservation of fossils in the Chagres sandstone marlins could shows in the next years important information about the evolution of billfishes. There are isolate bones, complete rostrum and skulls that will be published and excavation works will continue during the next years.

The evolution of billfishes includes convergent evolution of giant size between *M. nigricans* and *Is. indica* that could be possible by the beginning of the modern upwelling regimes across the world's ocean (Santini & Sorenson 2013). This has leaded the reorganization of pelagic communities and increase the availability of preys for this fishes (Jacobs *et al.* 2004; Rabosky & Sorhanus 2009; Santini & Sorenson 2013). The Late Miocene marlins linages appear to be as diverse as modern linages and our analyses including revision of some specimens (not included here) indicate that Miocene istiophorids could represent different assemblages to the modern istiophorids (Santini & Sorenson 2013). The extinct assemblage could be affected by the ocean reorganization and the collapse of the marine productivity during the Closure of the Central American seaway (Coates &

Stallard 2013; Montes *et al.* 2015; O'Dea *et al.* 2016). More recent Pliocene fossils and spearfishes indicate a second period of istiophorid diversification where appear some of the moderns species and could be related with body size reduction (Fierstine 2006; Santini & Sorenson 2013). This second speciation process could involve elongation and elevation of the skull, reduction of the temporal and pterotics crests, losing mineralization, losing ossification of skull, reductions of the vomer, lower jaw elongation of the body and convergent evolution of *Is. indica* (Nakamura 1985; Davie 1990; Colette *et al.* 2006; Santini & Sorenson 2013; Habbeger 2014).

CHAPTER SEVEN

PALEOECOLOGY AND PALEOBIOGEOGRAPHY

8.1 Paleoecology

Fierstine (2006) suggest that istiophorid billfish had similar preferences and distributional patterns to extant species. They are knows to be primarily oceanic and epipelagic with preference for water layers above the thermocline and by having the capacity to dive in greater depths (Collette *et al.* 2006; Pepperell 2010). Mynhier (2015) using gravimetry and Hendy *et al.* (in review) with analysis of mollusk faunas suggest that Chagres sandstone is the deepest zone of the Chagres – Gatun Basin arguing a mid-outer shelf environment. This assumption and the associated fish fauna represented by lantern fishes (Myctophidae) (De Gracia *et al.* 2012; Schwarhanz & Aguilera 2013) and sharks (Carrillo – Briceño *et al.* 2015) suggest a bathyal zone about ~370m as mean depth (Perez *et al.* 2017). Pyenson *et al.* (2015) using the fish assemblage from Río Indio facies (Aguilera & Rodrigues de Aguilera 1999) and unpublished data suggest neritic environment for Chagres sandstone arguing that lantern fishes are also abundant in shallow water sediments. But the fish assemblage they used not corresponds with the Chagres sandstone fauna in Piña (De Gracia *et al.* 2012; Schwarhanz & Aguilera 2013; Carrillo Briceño *et al.* 2015) and belongs to a lower layer (Collins *et al.* 1999) with age about 7.64 Ma (based in $^{87}Sr/^{86}Sr$ isotopes) (Hendy *et al.* in review). Additionally isotopic analysis of rare earth elements carried out on the specimen STRI 31291 and sharks teeth from the Chagres sandstone suggest that the digenesis of these fossils occurs about ~175 – 300 m (MacFadden *et al.* 2015). This result is agreed with the analysis of shark assemblage (Carrillo – Briceño *et al.* 2015; Perez *et al.* 2017) but we suggest a minimum depth of 200m for the water column as requirement for billfishes. The associate vertebrates in Chagres Sandstone include Squaliformes (that represents about ~70% of the sharks fauna) (Carrillo – Briceño *et al.* 2015), cetaceans as Kogids (Velez – Juarbe *et al.* 2015), Physesteroids (Vigil & Laurito 2014), and delphinoids (Pyenson *et al.* 2015) that further the presence of cephalopods (Nakamura 1985; Velez – Juarbe *et al.* 2015). Such vertebrate abundance indicates fish shoals and sharks schools [e.g. the benthopelagic shark *Isistius* sp. is the most abundant taxa in Chagres sandstone and is a facultative ectoparasite on large pelagic animals such billfishes and cetaceans (Campagno 1984; Carrillo – Briceño *et al.* 2015)] doing daily vertical migrations in oceanic upwelling system during the night (De Gracia *et al.* 2012; Carrillo – Briceño *et al.* 2015). The large eyes of billfishes are well adapted to low light levels and its unique thermoregulatory abilities are thus thought to increase the prey capture success in cold, dark waters during the day and in the monolith surface layer at night (Davie 1990; Fritsches *et al.* 2003; Barun *et al.* 2015). Despite having these adaptations, the intense productivity during the Late Miocene in the Caribbean caused by seasonality (O'Dea *et al.* 2007) could have compressed the thermocline (Pyenson *et al.* 2015) producing a temperature reduction on the water surface layers. Water temperature is an important environmental factor, which influence distribution of billfishes and drive seasonal migrations (Worn *et al.* 2005; Beyonce *et al.* 2008; Shimose *et al.* 2010). Also temperature is related with the distance billfish locates from the coastline and its preys (Nakamura 1985; Shimose *et al.* 2010). This limiting factor could produce a non-suitable habitat for billfishes throughout the year and the aggregations in the Panama volcanic arc could be seasonal (Fierstine 1999). Other works in progress suggest that istiophorids are the most abundant macrovertebrate taxa in Chagres sandstone. This abundance can be explained by the aggregation behavior that modern billfishes do around open ocean islands, far away atolls, waters around reef drops off or in waters over continental shelves for feeding or spawning (Pepperell 2010). In the case of Chagres sandstone, appears to be more a feeding area for istiophorids than spawning zone. This ecosystem can be compared today with Puerto Piñas, which belong to the Panama Gulf, and where about to 6-12 miles from the coast occurs sportfishing for billfish (Suman 2007). The distance from the coastline in Puerto Piñas to where billfish occurs geographically represents the beginning of the continental slope and waters with oceanic influence (Coates 1999b; D'Croz & O'Dea 2007, 2009). Today the presence of billfishes along the slope of the Pacific Shelf in Panama supports the idea that proximal open ocean environments influenced the neritic basins during the Late Miocene and that Chagres sandstone could be a short platform environment bordered by deep water (Carrillo – Briceño *et al.* 2015; Perez *et al.* 2017).

8.2 Paleogeography

Late Miocene is a period characterized by the swallowing of the Panama Arc and followed by the closure of the Central American Seaway (CAS) and the isolation of the Caribbean from the Pacific ocean (Coates *et al.* 2004; Farris *et al.* 2011; Montes *et al.* 2012; Montes *et al.* 2015; O'Dea *et al.* 2016; Farris *et al.* 2017). The Chagres Formation represents the youngest formation from the Panama Canal basin (Collins *et al.* 1996; Farris *et al.* 2017) and since the discovery of its rich marine vertebrate fauna being highly investigated. The Chagres sandstone has been called “the smoking gun” (Stone 2013) for the new models about the closure of the Central American Seaway and given its importance the interpretation of its faunal association is being debated (Montes *et al.* 2012; Coates & Stallard 2013; Stone 2013; Montes *et al.* 2015; O’Dea *et al.* 2016; Farris *et al.* 2017). The presence of billfishes and associates marine vertebrates in Chagres sandstone with its Messinian (5.8Ma) age is contrasting with the shallow water fauna from the Río Indio Member (Collins *et al.* 1996; Aguilera & Rodrigues de Aguilera 1999; Carrillo *et al.* 2015). The bathyal benthic foraminifera at the base of the Formation in the Toro member widely reported accumulating in bathyal depths associated with the deepening of the Panama isthmian strait (Bandy 1970; Collins *et* al. 1996; Coates *et al.* 2004) but the study of the mollusk fauna suggest more neritic environment (<50m for Toro, 25-75m for Rio Indio and 75-150 for Chagres sandstone) (Hendy *et al.* in review). The lateral replacement of Toro Member by Rio Indio facies and its unconformable lower contact with Gatun Formation (Tortonian) (Hendy *et al.* 2013) suggest a big shallow basin, which maintained the marine connections between Caribbean and Pacific (Pimiento *et al.* 2013; Perez *et al.* 2017). Gravimetric analysis suggest that the deepest zone of this basin was located where is approximately the Toro Member and that this place is the most probable location for a Connections between Pacific and Caribbean by the Middle Late Miocene (Mynhier 2015). By the Messinian Chagres formation is represented by a deepening in the Chagres sandstone but this process cannot be explained by sea – level changes and must therefore have been due to subsidence by volcanic activity (O’Dea *et. al.* 2016; Farris *et al.* 2017). Collins *et al.* (1999) infers that Chagres was deposited adjacent to a jet of the North Equatorial Countercurrent - Equatorial Undercurrent that is formed as it passed through the narrow Panama isthmian strait. This mechanism can explain the nature of the upwelling, the associate fish fauna and a well-oxygenated water column that could allow the presence of benthic bioturbation.

CHAPTER EIGHT

CONCLUSION

After review of all fossil species of istiophorid billfishes and comparison with recent material was possible establish a detailed reorganization of its taxonomy. There are 7 fossil species of istiophorid including the new two species here described. *I. solidus* was excluded of the family Istiophoridae and translated to *Xiphiorhynchus* (Xiphiidae: Xiphiorhynchinae) where was described in previous works. We detected that *M. teretirostris* was misidentified is a junior synonym of *M. nigricans*.

We used the rostral variables established by Fierstine & Voight (1996) and we compared it method with our PCA analysis and we found that rostral variables are able to discriminate between different genera and species. In this work we used for first time a model for data imputation with MAR missing data for anatomical variables and applied its result for comparison with fossils. Given the high levels of correlation between the variables our method resulted in very effective technique to deal with missing data and its use in paleontology is effective when the taxon studied have living representatives. The only limitation in this technique is that we not included spearfishes (*Tetrapturus*) and we had few specimens of *Istiompax indica*. But is expected that the result improve in the way more individuals are added.

Of the non - rostral variables we concluded that can be used for study billfishes but the predentarium and the first pectoral fin ray do not show any differences in our analysis. The only species that can be discriminated with the first pectoral fin ray is *Istimpax indica* given its unique shape. We found that bones involved in feeding function as dentaries, articular and rostrum bones, vomer, parasphenoid, basioccipital have phylogenetic importance. Other important variables are the pectoral fin girdle, the shape of the neural spine in the caudal vertebrae and the vertebrae that forms the caudal peduncle.

The Chagres sandstone represents a very rich marine fossil vertebrate and the richest fossil fauna for Central America. The billfishes preserved in its sediments are the most complete and best preserved ever discovered and are key to understand the modern billfish and its evolution. Whit the records presented here and the taxonomic revision we believe that Late Miocene istiophorids represent a different assemblage with the exception of *M. nigricans*. The rest of the living istiophorid have youngest records for the Early Pleistocene. These differences indicates that the global ocean reorganization may be derived the evolution of modern species assemblage of istiophorids.

Istiophorid are the most abundant macrovertebrate taxon in the Chagres sandstone and its associate fauna and isotopic analysis suggest that were deposited in a water column with a minimum 200m depth and not less of this. The median depth suggests using sharks suggest 370m and this environment represent a short platform with oceanic upwelling. The istiophorids however could be limited by the seasonal variation of the temperature and is less probable that they were permanent resident in the Panama arc during the Late Miocene and that this aggregation is the result of annual migrations as occurs nowadays. This new data could have implications to understand the process of closure of the CAS during the Late Miocene and the billfish fauna presented here adjust more to a late closure of the CAS.

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TABLES

Table 1. Selected measures for the specimens: STRI 31291 and STRI 31293. See text for definition of abbreviations. Approximately 13mm were added to the long of the bill in (STRI 31293) and measures for W2 and H2 were estimated filling the missing space with plaster. Measure of the DAD for *Makaira* sp. (STRI 31291) was estimated from predentary PD data. Modified measures are indicated with asterisk (*).

Characters	Measurements (mm)	
	STRI 31291	STRI 31293
Rostrum		
L	551	624*
D1	21.7	29.96
W1	33.9	41.26
H1	5.5	6.54
N1	3.0	4.71
DD1	8.8	14.93
IC1	2.2	3.05
D2	18.4	24.32
W2	28.0	25.05*
H2	4.3	4.92 *
N2	2.0	3.32
DD2	7.5	12.41
IC2	4.2	3.24
P	155	148
VSPM	320	248
Neurocranium		
ACW	83.0	-
PTW	167.44*	-
CAL	263.0	-
Predentary		
PL	50.24	-
PW	30.19	-
PD	18.01	-
Dentary		
DAD	18.01*	21.0
DJL	44.85	40.3
Articular		
ASM	35.63	-
AL	20.69	-
AAL	17.78	-
ATW	17.08	-
AW	18.76	
1st pectoral ray		
FW	33.85	-
FAW	18.84	-
Vertebra 14		
CL	94.0	-
NH	92.0	-
NL	90.0	-
Vertebra 22		
CL	58.13	-
VPD	17.15	-
Vertebra 23		
CL	50.48	-
VPD	21.74	-

Table 2. Mean (x), observed range, and number of specimen examined (n) for 9 rostral variables and five bones of eight extant fish species of the family Istiophoridae compared with STRI 31291 and STRI 32293. Abbreviations of the ratio are explained on the methodology and the legend of the figures 3-5. Data have been taken of Fierstine 2001.

Table 2. Mean (x), observed range, and number of specimen examined (n) for 9 rostral variables and five bones of eight extant fish species of the family Istiophoridae compared with STRI 31291 and STRI 32293. Abbreviations of the ratio are explained on the methodology and the legend of the figures 3-5. Data have been taken of Fierstine 2001.

Character	*I. platypterus* (x) (range) n	*Is. indica* (x) (range) n	*M. nigricans* (x) (range) n	*T. albidus* (x) (range) n	*T. angustirostris* (x) (range) n	*T. audax* (x) (range) n	*T. pfluegeri* (x) (range) n	*T. belone* (x) (range) (n)	*STRI 32291* (x) (range) n	*STRI 32293* (x) (range) n
Rostrum										
D1/W1	.68 (.58-.78) 31	.72 (.66-.78) 10	.70 (.59-.80) 41	.62 (.56-.66) 13	64(.57-.70) 3	.68 (.59-.80) 13	.62 (.59-.64) 2	-	.64	.73
H1/D1	.24 (.15-.35) 28	.16 (.13-.20) 9	.14 (.07-.20) 36	.13 (.09-.15) 7	-	.14 (.10-.17) 8	-	-	.25	.22
DD1/D1	.32 (.21-.41) 28	.43 (.38-.49) 9	.46 (.33-.62) 36	.40 (.35-.45) 7	-	.11 (.08-.14) 7	-	-	.41	.50
D2/W2	.64 (.55-.75) 30	.68 (.58-.77) 10	.64 (.54-.83) 41	.53 (.47-.61) 14	.61 (.58-.64) 3	.61 (.52-.67) 13	.65 (.65) 2	-	.66	.97
H2/D2	.18 (.11-.26) 28	.10 (.08-.12) 9	.12 (.06-.21) 32	.12 (.09-.14) 7	.11 (.07-.14) 2	.12 (.09-.14) 8	- (.15) 1	-	.23	.20
DD2/D2	.38 (.28-.46) 28	.46 (.38-.51) 9	.47 (.22-.64) 32	.40 (.32-.43) 7	.63 (.62-.63) 2	.46 (.41-.55) 8	.49 (.48-.50) 2	-	.41	.50
D2/VSPM	.03 (.03-.04) 25	.06 (.05-.08) 8	.04 (.04-.05) 35	.04 (.03-.05) 12	.15 (.13-.19) 3	.04 (.03-.05) 12	.05 (.05-.06) 2	-	.06	.10
W2/VSPM	.05 (.04-.06) 24	.09 (.07-.10) 8	.07 (.05-.08) 35	.07 (.06-.09) 12	.24 (.20-.30) 3	.06 (.05-.08) 12	.08 (.07-.09) 2	-	.09	.10
P/VSPM	.58 (.45-.83) 17	.53 (.48-.60) 8	.51 (.38-.87) 33	.53 (.42-.66) 11	.39 (.30-.45) 3	.48 (.38-.57) 12	.55 (.55-.56) 2	-	.48	.60
Dentary										
DAD/DJL	.44 (.33-.55) 15	- (.86) 1	.76 (.55-.89) 12	.53 (.47-.60) 10	-	.56 (.39-.74) 7	.26 (.22-.30) 2	-	.40	.52
Predentary										
PW/PL	.50 (.23-.63) 21	.54 (.48-.62) 5	.65 (.45-1.1) 23	.41 (.34-.57) 15	.60 (.54-69) 4	.42 (.33-.51) 13	- (.65) 1	- (.59) 1	.60	-
PD/PL	.27 (.20-.37) 21	.38 (.30-.41) 5	.36 (.26-.58) 23	.24 (.20-.33) 15	.59 (.52-69) 4	.26 (.22-.30) 13	- (.60) 1	- (.53) 1	.36	-
PD/PW	.56 (.48-1.0) 21	.70 (.63-.81) 5	.56 (.48-.61) 23	.59 (.53-.65) 15	.99 (.97-1.0) 4	.60 (.53-.72) 13	- (.92) 1	- (.90) 1	.60	-
Articular										
AL/ASM	.70 (.59-.80) 22	.90 (.85-.94) 2	.80 (.66-.93) 23	.71 (.58-.91) 15	-	.78 (.68-.88) 9	- (.81) 1	-	.58	-
AW/AL	.74 (.53-.94) 22	.70 (.69-.70) 2	.84 (.68-1.1) 23	.91 (.65-1.3) 15	-	.71 (.58-.85) 9	- (.89) 1	-	.91	-
AAL/AL	.74 (.59-.92) 22	.59 (.59-.60) 2	.68 (.47-.91) 23	.70 (.54-.97) 15	-	.66 (.55-.79) 9	- (.29) 1	-	.86	-
ATW/AL	1.1 (.91-1.4) 21	.94 (.94-.95) 2	1.2 (.98-1.6) 22	1.3 (.96-1.9) 15	-	1.1 (.87-1.3) 9	- (1.1) 1	-	.83	-
AW/ATW	.67 (.54-.78) 26	.74 (.74-.74) 2	.71 (.52-.78) 22	.71 (.57-.86) 15	-	.63 (.58.70) 10	- (.81) 1	-	1.1	-
1st pectoral fin ray										
FAW/FW	.65 (.55-.71) 17	.27 (.18-.37) 8	.65 (.51-.72) 20	.66 (.61-.72) 14	- (.62) 1	.62 (.58-.67) 4	- (.65) 1	- (.72) 1	.56	-
Vertebra 22										
VPD/CL	.49 (.45-.54) 11	- (.50) 1	.48 (.45-.51) 7	.48 (.46-.50) 4	-	.54 (.51-.57) 2	- (.40) 1	-	.30	-
Vertebra 23										
VPD/CL	.50 (.42-.63) 10	- (.50) 1	.52 (.44-.59) 6	.53 (.48-.59) 6	- (.43) 1	.54 (.52-.56) 2	- (.42)1	-	.43	-

Table 3. Score sheet for species identification of 9 ratios studied for the rostrum and 11 ratios studied of 6 bones for 8 modern istiophorid species. The first number is the number of ratios on the range for *Makaira* n. sp. 1 and the second number is the total of analyzed ratios of each bone. The total score indicates the number of ratios of STRI 31291 on the rage for each modern species.

Billfish species	Bone							Total score
	Rostrum	Dentary	Predentary	Articular	1st spine	V22	V 23	
I. platypterus	7/9	1/1	3/3	2/5	1/1	0/1	1/1	15
Is. indica	7/9	?	3/3	0/5	0/1	0/1	?	10
M. nigricans	5/9	0/1	3/3	2/5	1/1	0/1	0/1	11
K. albida	5/9	0/1	1/3	3/5	0/1	0/1	0/1	9
K. audax	4/9	1/1	1/3	1/5?	0/1	0/1	0/1	7
T. angustirostris	1/9	?	1/3	?	?	0/1	1/1	3
T. pfluegeri	5/9	0/1	1/3?	?	?	0/1	1/1	7
T. belone	?	?	1/3?	?	?	0/1	?	1
Out range values	0/9	0/1	0/3	2/5	0/1	1/1	0/1	3

Table 4. Score sheet for species identification of 9 ratios studied for the rostrum and 1 ratio of the dentary of 7 modern billfish species. The first number is the number of ratios on the range for *Makaira* n. sp. 2 and the second number is the total of analyzed ratios of each bone. The total score indicates the number of ratios of STRI 31293 on the rage for each modern species.

Billfish species	Bone		Total score
	Rostrum	Dentary	
I. platypterus	4/9	1/1	5
Is. indica	4/9	?	4
M. nigricans	5/9	0/1	5
K. albida	1/9	1/1	2
K. audax	2/9	1/1	3
T. angustirostris	2/9	?	2
T. pfluegeri	0/9	0/1	0
Out range values	1/9	0/1	1

FIGURES

Figure 1. a – c, Location map; stratigraphy and geological setting of the type locality (Piña, Chagres district, Costa Abajo, Colon Panama). Stratigraphic column is not in vertical scale. Taken and modified of Collins *et al.* (1996).

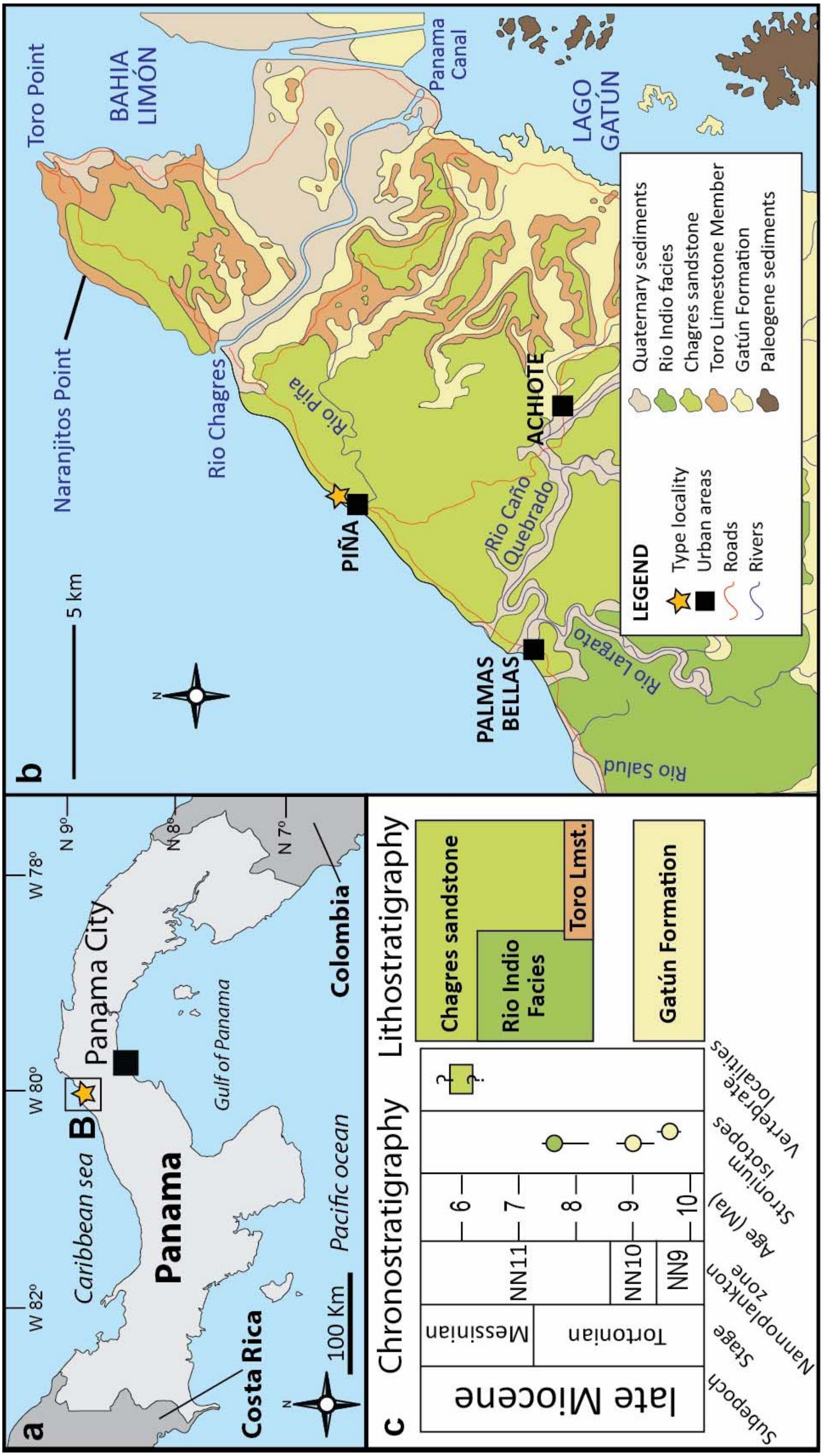

a
Costa Rica
Panama
Caribbean sea
Pacific ocean
Gulf of Panama
Panama City
Colombia
B
100 Km
N
W 82°
W 80°
W 78°
N 9°
N 8°
N 7°
b
5 km
N
Toro Point
BAHIA LIMÓN
Panama Canal
LAGO GATÚN
Naranjitos Point
Rio Chagres
Rio Piña
PIÑA
ACHIOTE
Rio Caño Quebrado
PALMAS BELLAS
Rio Largato
Rio Salud
LEGEND
Type locality
Urban areas
Roads
Rivers
Quaternary sediments
Rio Indio facies
Chagres sandstone
Toro Limestone Member
Gatún Formation
Paleogene sediments
c
Chronostratigraphy
Lithostratigraphy
late Miocene
Messinian
Tortonian
NN11
NN10
NN9
6
7
8
9
10
?
Chagres sandstone
Rio Indio Facies
Toro Lmst.
Gatún Formation
Subepoch
Stage
Nannoplankton zone
Age (Ma)
Strontium isotopes
Vertebrate localities

Figure 2. Stratigraphic column of Piña showing the fossiliferous strata. Taken and modified of Coates (1999).

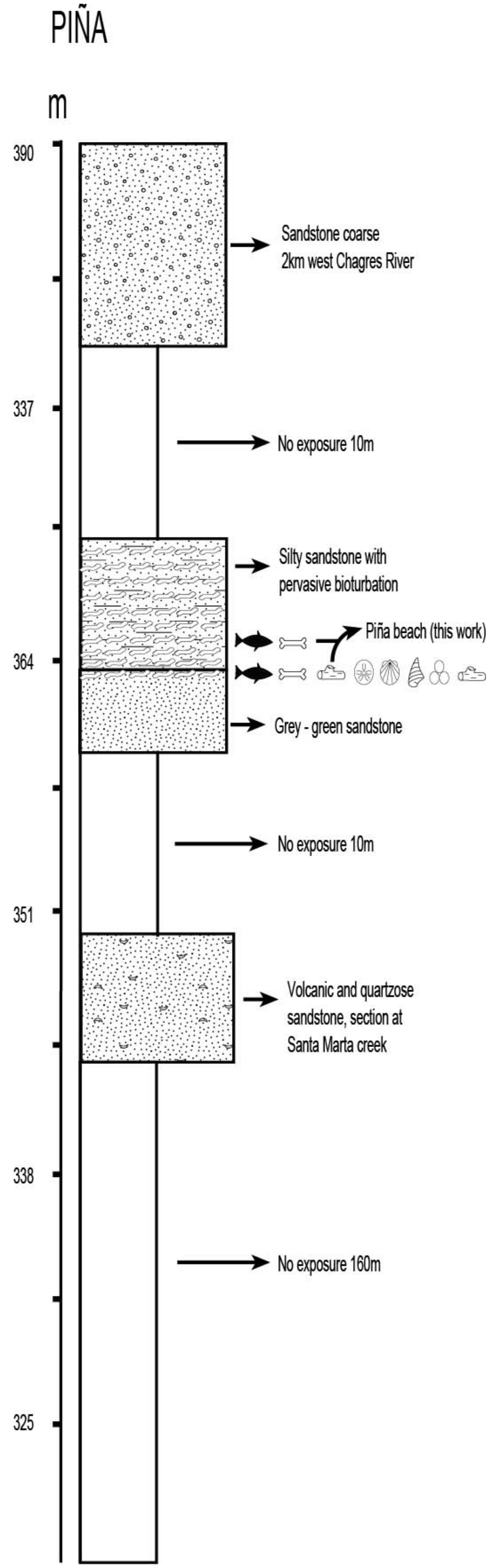

PIÑA
m
390
Sandstone coarse
2km west Chagres River
337
No exposure 10m
Silty sandstone with
pervasive bioturbation
Piña beach (this work)
364
Grey - green sandstone
No exposure 10m
351
Volcanic and quartzose
sandstone, section at
Santa Marta creek
338
No exposure 160m
325

Figure 3. Picture in Piña town beach showing the Chagres sandstone sediments with the pervasive arthropods burrows.

Figure 4. A generalized istiophorid rostrum (modified from Fierstine and Voigt, 1996): **a**, left lateral view; **b**, dorsal view; **c**, ventral view. Abbreviations: i pr = internal process, m pr = maxillary process, ORB = orbital region, tr = triangular region of maxilla. See anatomical abbreviations for bone names. Taken and modified from Fierstine & Voight (1996).

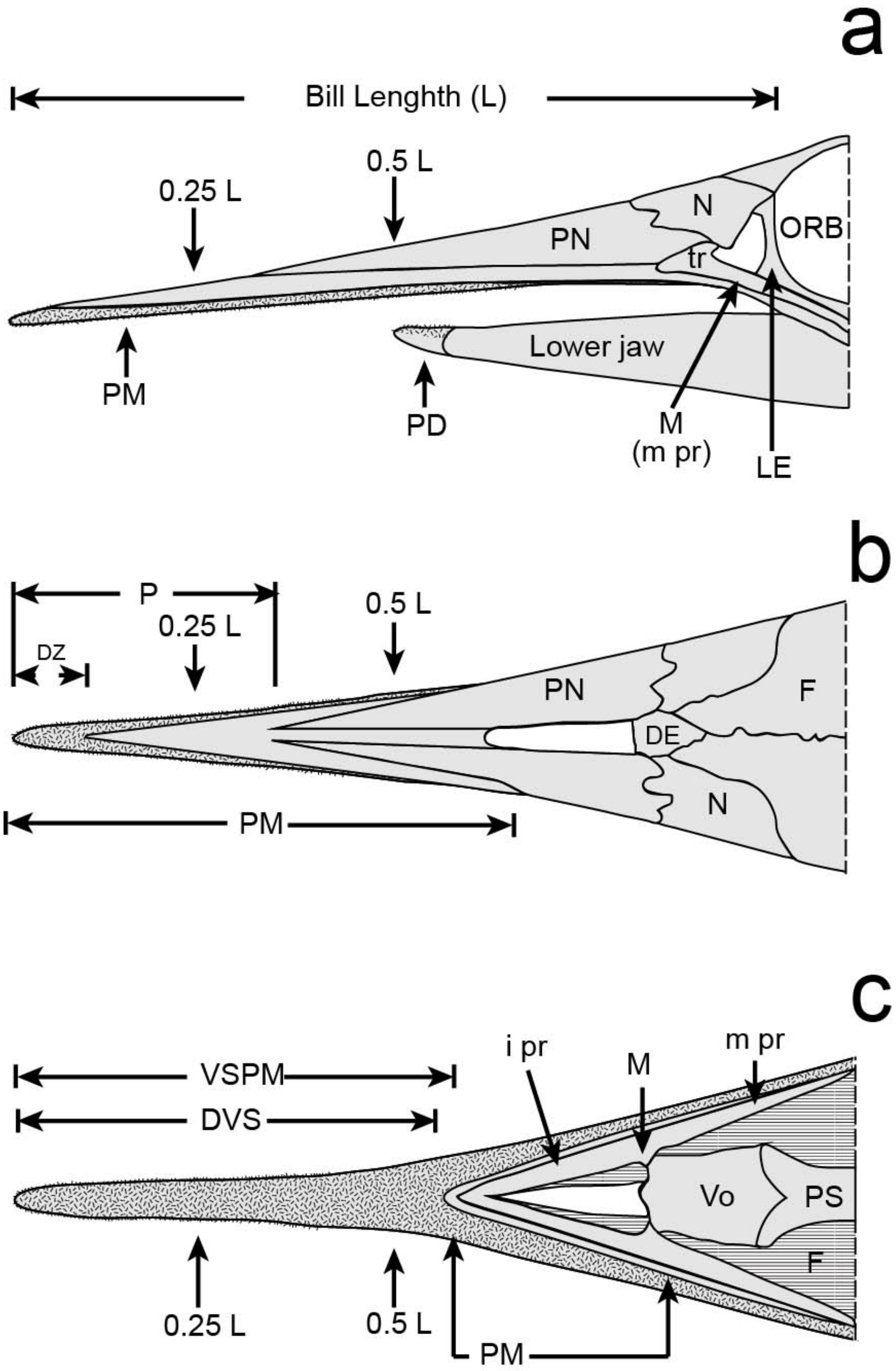

a
Bill Lenghth (L)
0.5 L
0.25 L
N
PN
ORB
tr
Lower jaw
PM
PD
M
(m pr)
LE
b
P
0.25 L
0.5 L
DZ
PN
F
DE
N
PM
c
i pr
M
m pr
VSPM
DVS
Vo
PS
F
0.25 L
0.5 L
PM

Figure 5. **a-h**; generalized istiophorid rostrum, cranial and neural spine variables. **a**, cross section variables of a generalized istiophorid rostrum at one – half bill length (0.5L); **b**, cross section variables of a generalized istiophorid rostrum at one – fourth bill length (0.25L); **c**, ventral view of neurocranium showing the cranial variables that defines the skull shape; **d**, neural spine of the 14th vertebra of billfishes; **e**, shape variation of the neural spine in caudal vertebrae for different billfish genera (better observed in the 14th vertebra): square neural spine in *Makaira* and *Istiompax*; triangular neural spine in *Istiophorus*; rhomboid shape in *Kajikia*; rectangular shape in *Tetrapturus*. See characters section and anatomical abbreviations for names. Taken and modified of Fierstine & Voight (1996) and Nakamura (1983).

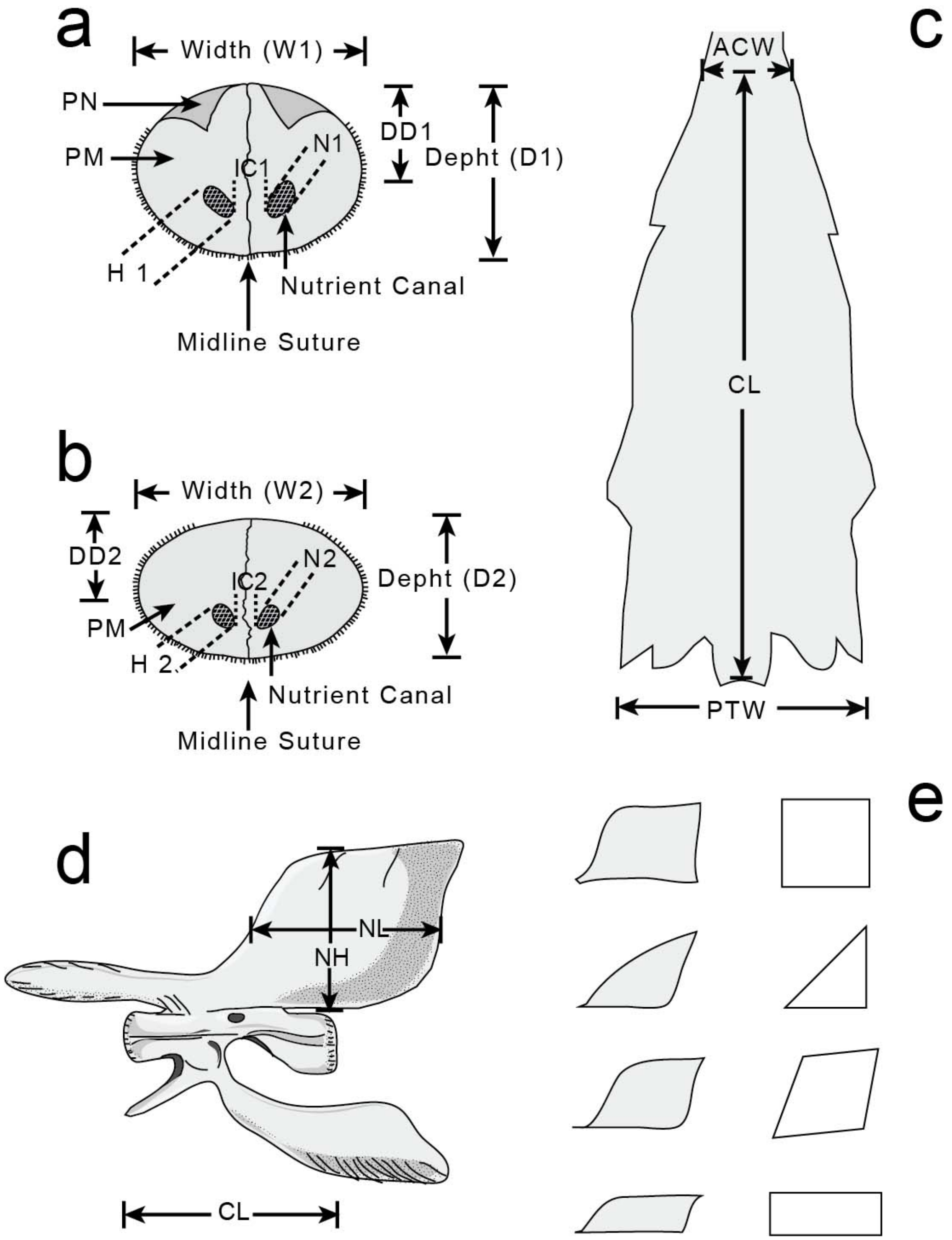

a
Width (W1)
PN
PM
DD1
Depht (D1)
N1
IC1
H 1
Nutrient Canal
Midline Suture
b
Width (W2)
DD2
Depht (D2)
N2
IC2
PM
H 2
Nutrient Canal
Midline Suture
c
ACW
CL
PTW
d
NL
NH
CL
e

Figure 6. Bones of a generalized istiophorid: **a**, left dentary, medial view of interdentary joint; **b**, twenty – second vertebra, left lateral view; **c**, left articular, lateral view of posterior region; **d**, left articular dorsal view of joint with quadrate; **e**, left first pectoral – fin ray, proximal view emphasizing articular facet for scapula; **f**, predentary, dorsal view; **h** left lateral view. Abbreviation: mf = mandibular foramen, sf = spinal foramen, Q-A = socket of quadrate – articular joint. See characters for definition of other abbreviations. Taken and modified of Fierstine (2001).

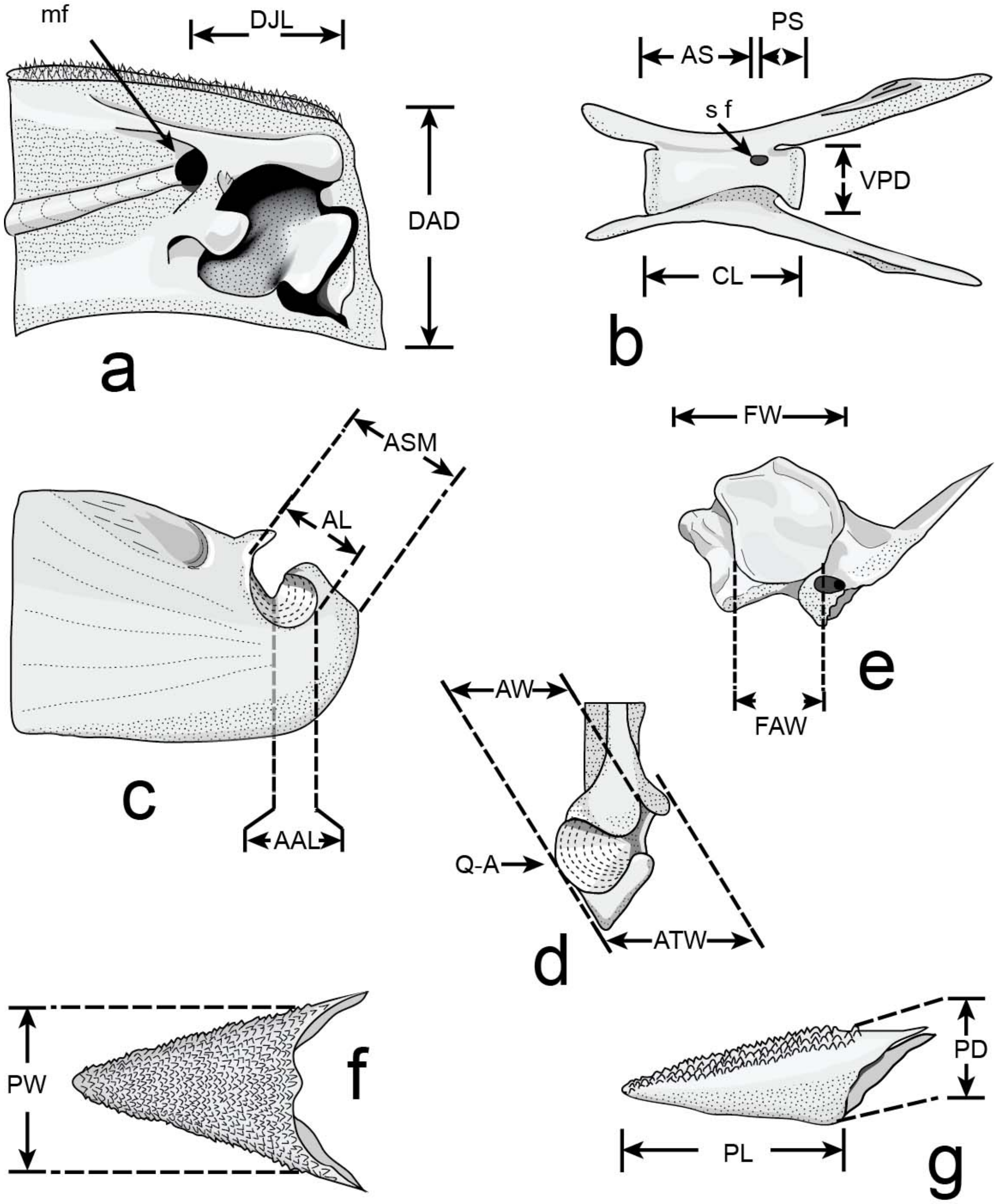

mf
DJL
DAD
a
AS
PS
s f
VPD
CL
b
ASM
AL
AAL
c
FW
FAW
e
AW
Q-A
ATW
d
PW
f
PD
PL
g

Figure 7. a-c; position of the nutrient canals respect to the midline formed by the suture of the two premaxillaries: a; medial; b, dorsal; c, ventral. d-f; lateral distribution of the nutrient canals: d; centrally distributed, e; laterally distributed; f, intermediated distributed. g-I; rotation of the internal canals: g; dextrogyre; h, parallels; I, levogyre.

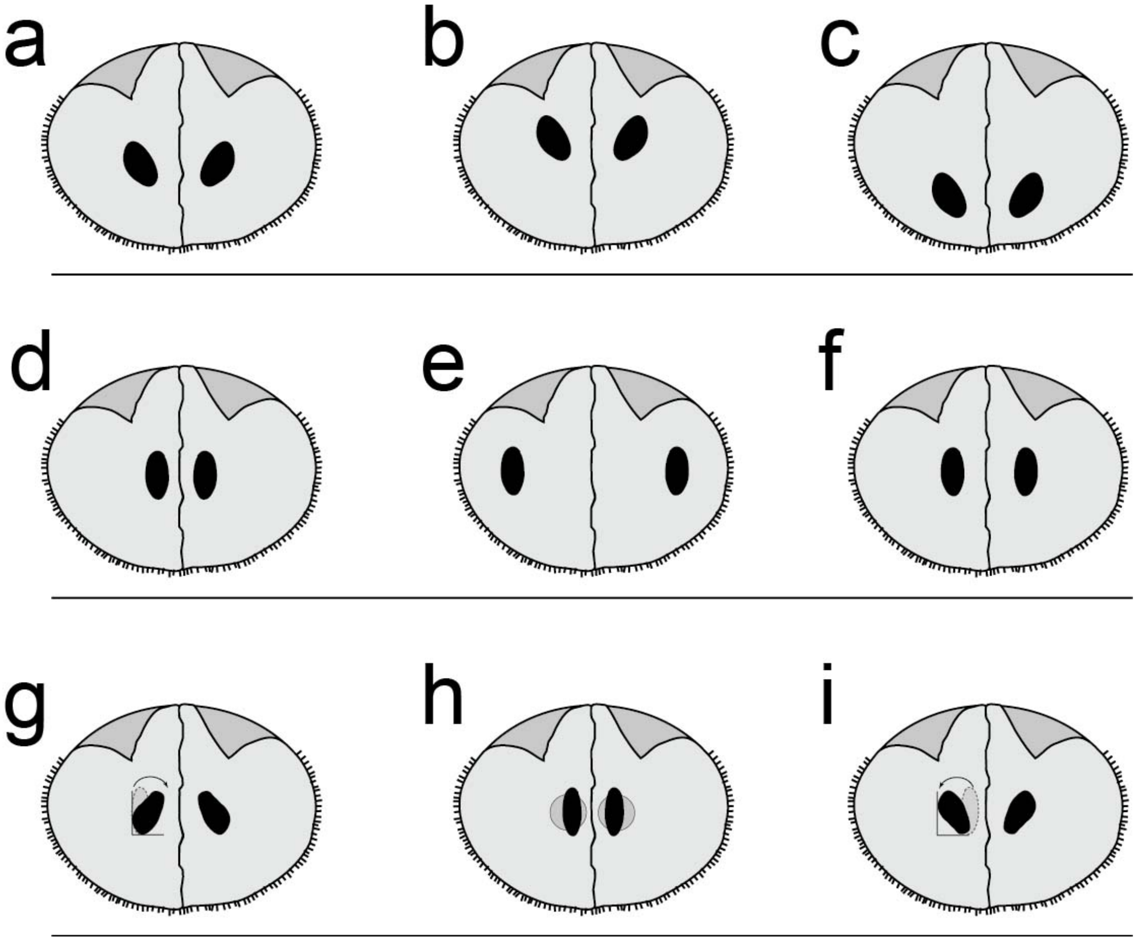

a
b
c
d
e
f
g
h
i

Figure 8. **a-f**; distal tip variation in istiophorid fishes: **a**; globular (bulled shape) distal tip in dorsal and lateral view; **b**, cross - section variation of the globular tip; **c**, slender (spear – shape) distal tip in dorsal and lateral view; **d**, cross - section variation of the slender tip; **e**, depressed (more or less plane) distal tip in dorsal and lateral view; **f**, cross section of the depressed tip. The cross section in the right represent the point where the prenasal suture is observed by last time and the cross-section at the right is indicated by the dashed line; both distal tips and the cross –sections are not in scale by better representation.

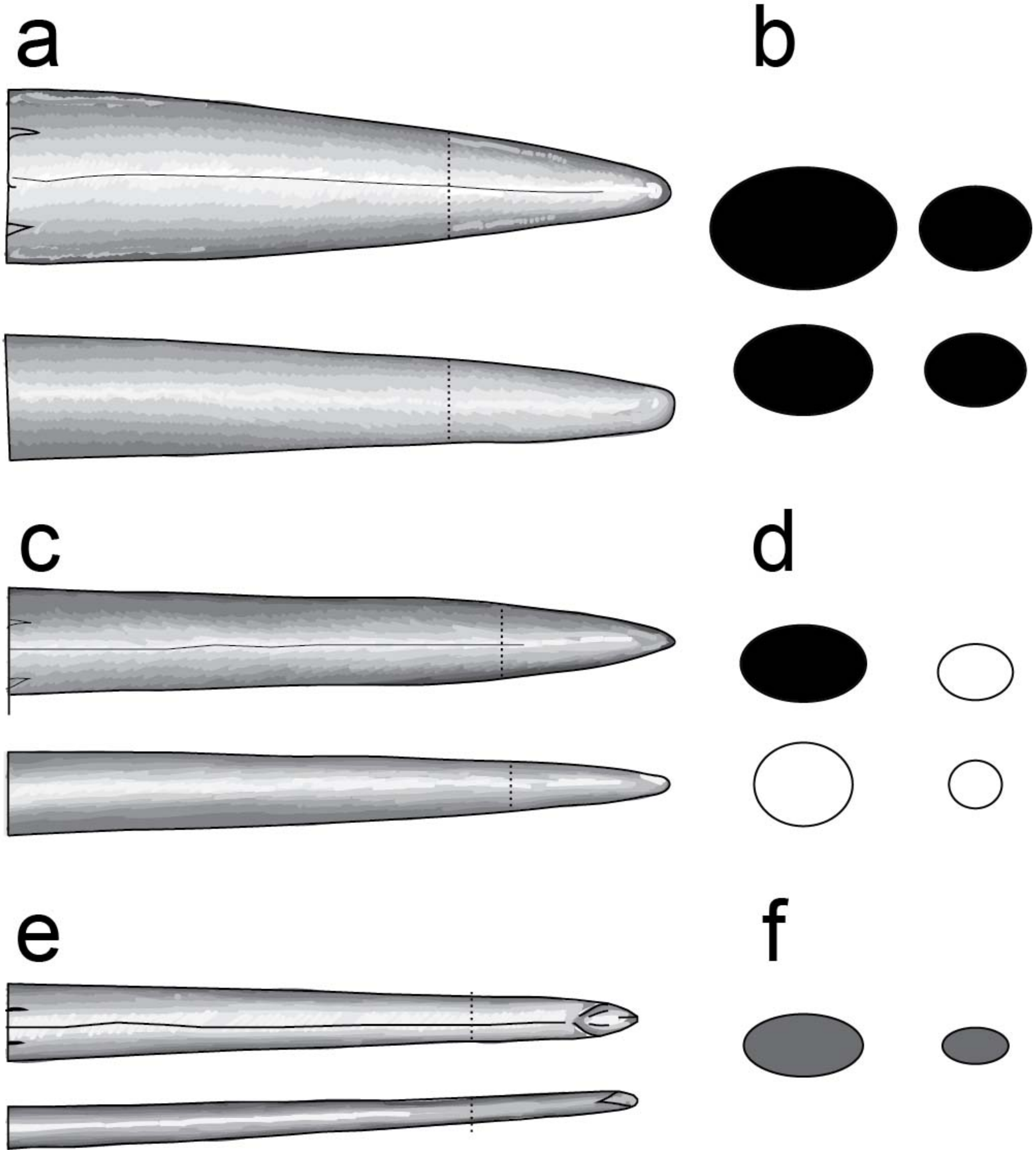

a
b
c
d
e
f

Figure 9. *Makaira?* sp. nov. *1* (STRI 31291); **a**, Adjoining blocks in natural arrangement containing the skeleton showing the complete specimen as preserved; **b**, first block with the description of the bones preserved in the anterior half of the specimen; **c**, second block with the description of the bones preserved in the posterior half of the specimen. Scale bar 20 cm. See anatomical abbreviations for bone names.

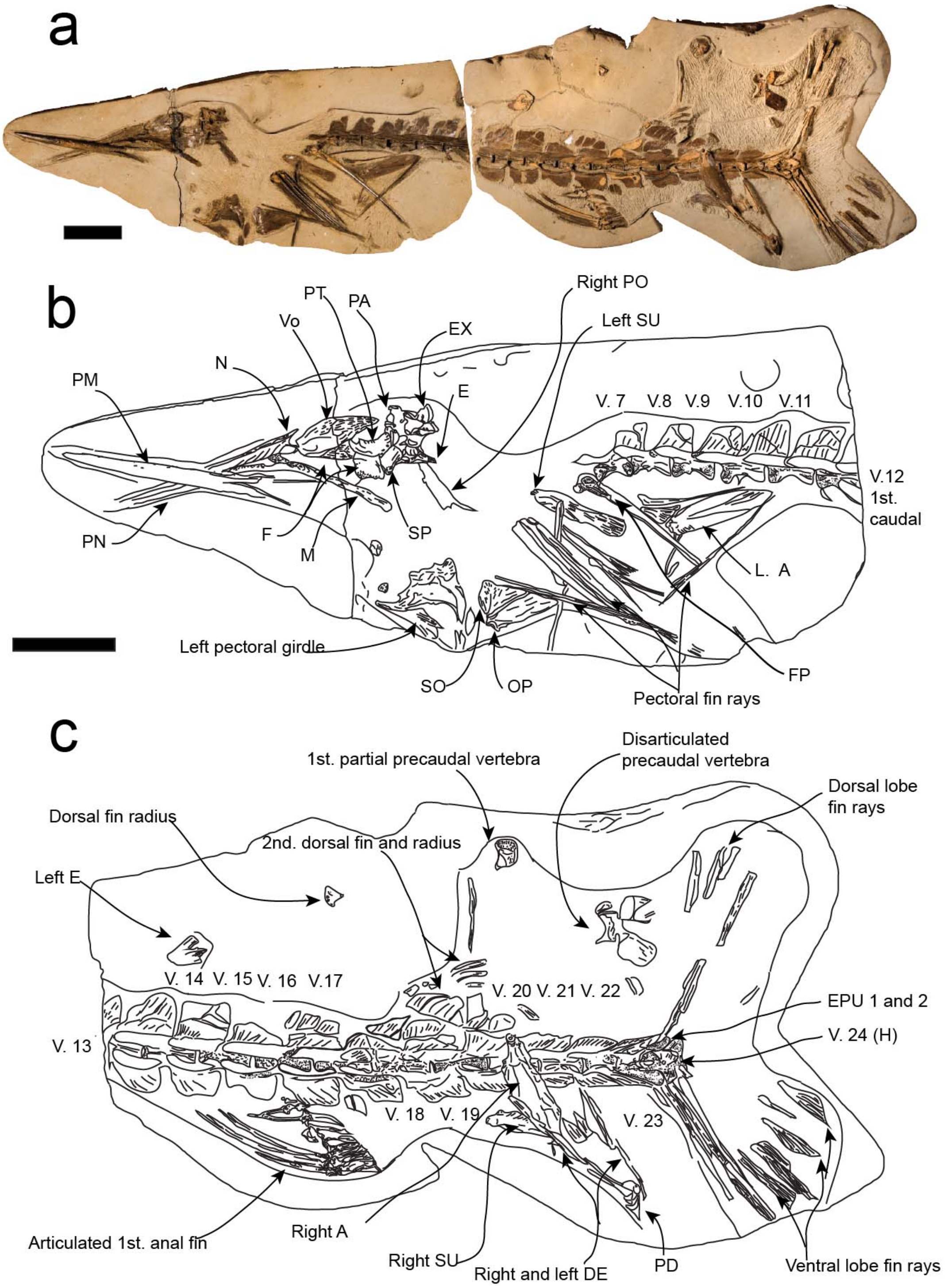

a
b
Right PO
Left SU
PT
PA
Vo
EX
N
E
PM
V. 7
V.8
V.9
V.10
V.11
V.12
1st.
caudal
PN
F
M
SP
L. A
Left pectoral girdle
SO
OP
FP
Pectoral fin rays
c
Disarticulated
precaudal vertebra
1st. partial precaudal vertebra
Dorsal lobe
fin rays
Dorsal fin radius
2nd. dorsal fin and radius
Left E
V. 14
V. 15
V. 16
V.17
V. 20
V. 21
V. 22
EPU 1 and 2
V. 13
V. 24 (H)
V. 18
V. 19
V. 23
Articulated 1st. anal fin
Right A
Right SU
Right and left DE
PD
Ventral lobe fin rays

Figure 10. **a – b**; Computer – tomography images of the cross – sections for the specimen *Makaira?* n. sp. 1 STRI 31291 at 0.5L and 0.25L distances respectively; **c – d**, pictures of the cross – sections cuts for the specimen *Makaira* n. sp. 2 STRI 31293 at the distances 0-5L and 0.25L respectively. Scale bar = 1 cm.

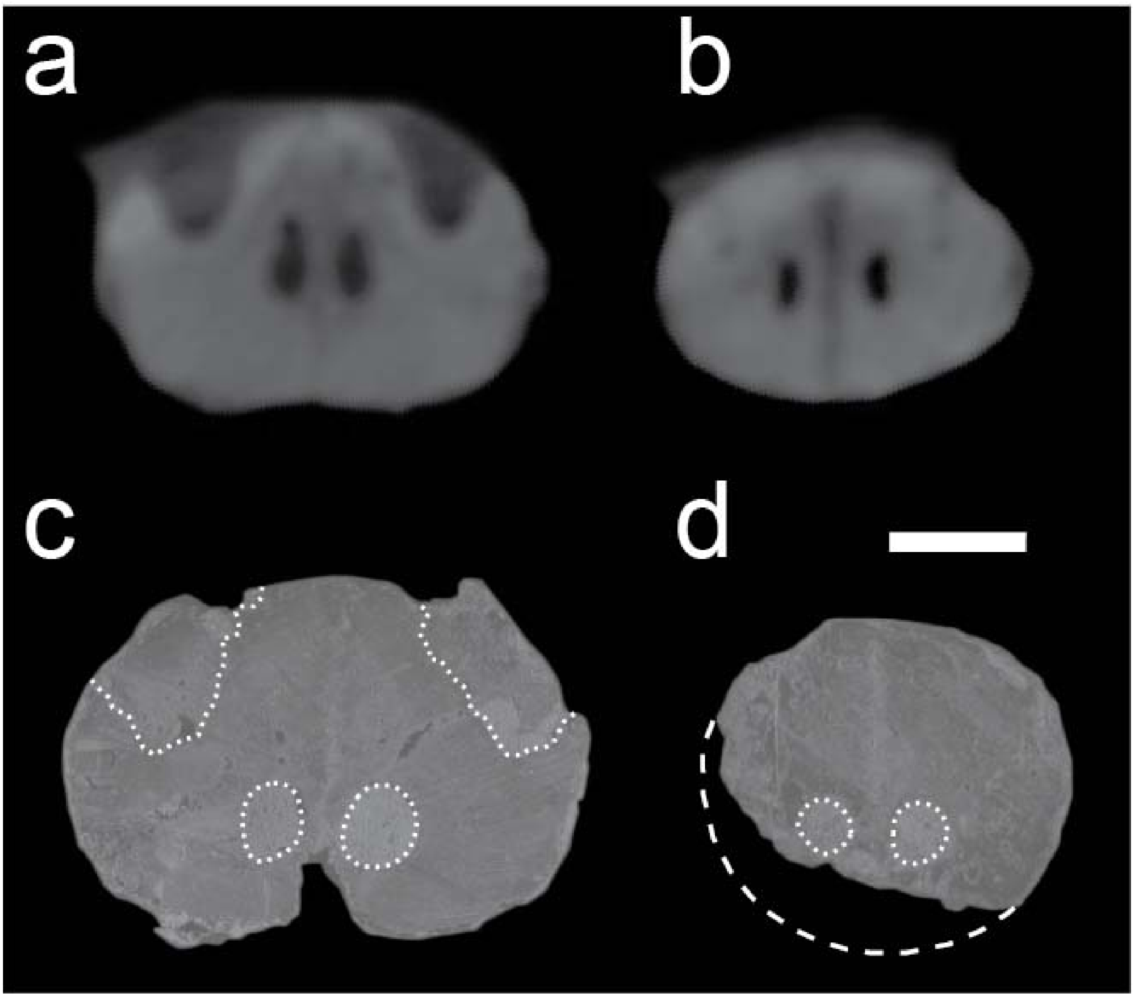

a
b
c
d

Figure 11. **a-b**; detail of the neurocranium of *Makaira* n. sp. 1 showing the cranium bones preserved; **c**, disarticulate rostrum in the first block showing the premaxillaries and the prenasals.

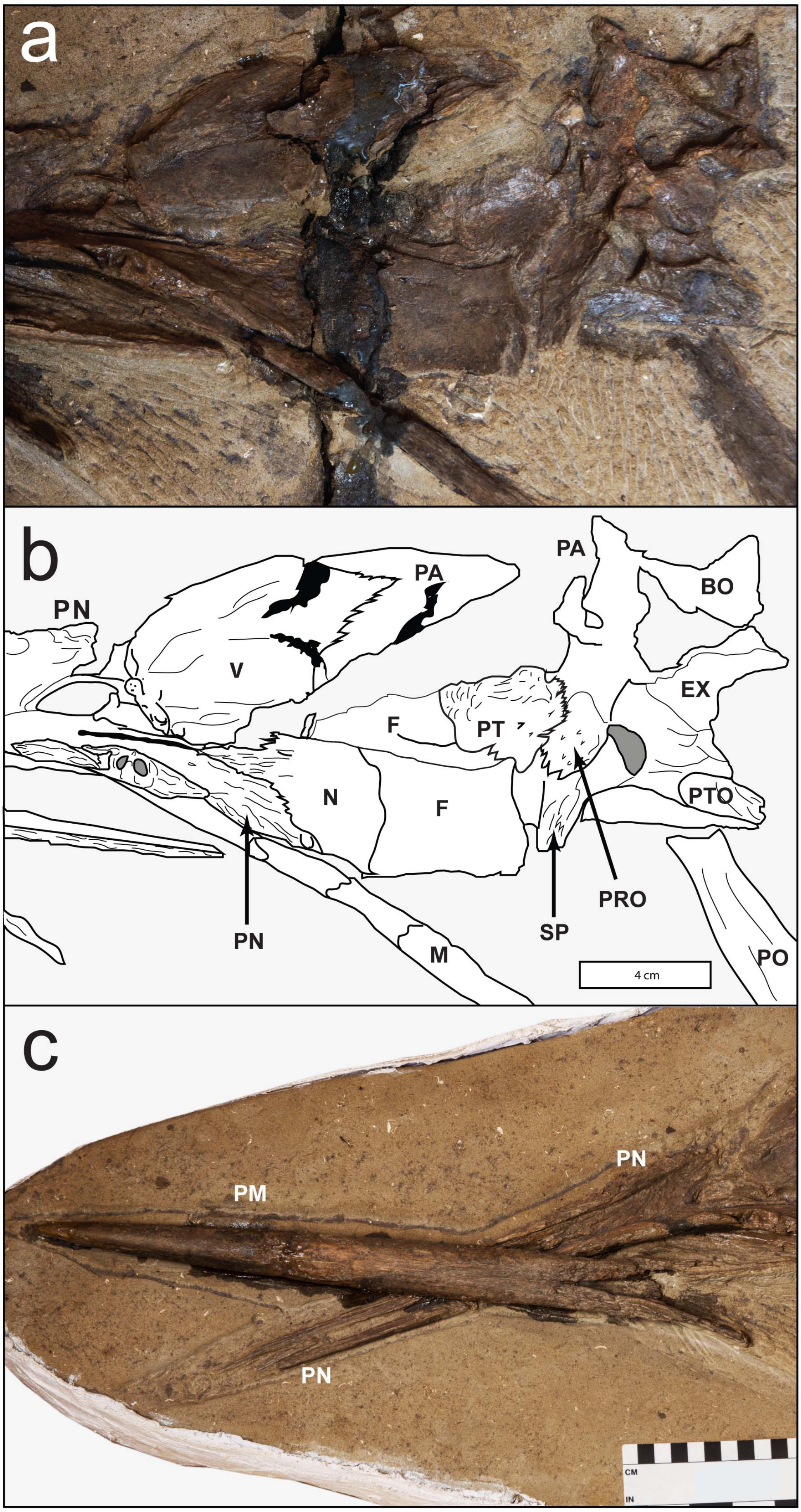

a
b
PN
PA
V
PA
BO
EX
F
PT
N
F
PTO
PN
SP
PRO
M
PO
4 cm
c
PN
PM
PN
CM
IN

Figure 12. **a – c**; Reconstruction of *Makaira* n. sp. 1 based in the preserved bones anatomy and the computer tomography; **a**, dorsal view of the skull; **b**, lower jaw reconstruction in dorsal view; **c**, lower jaw reconstruction in left lateral view.; d, Skull in ventral view. Scale bar = 8cm.

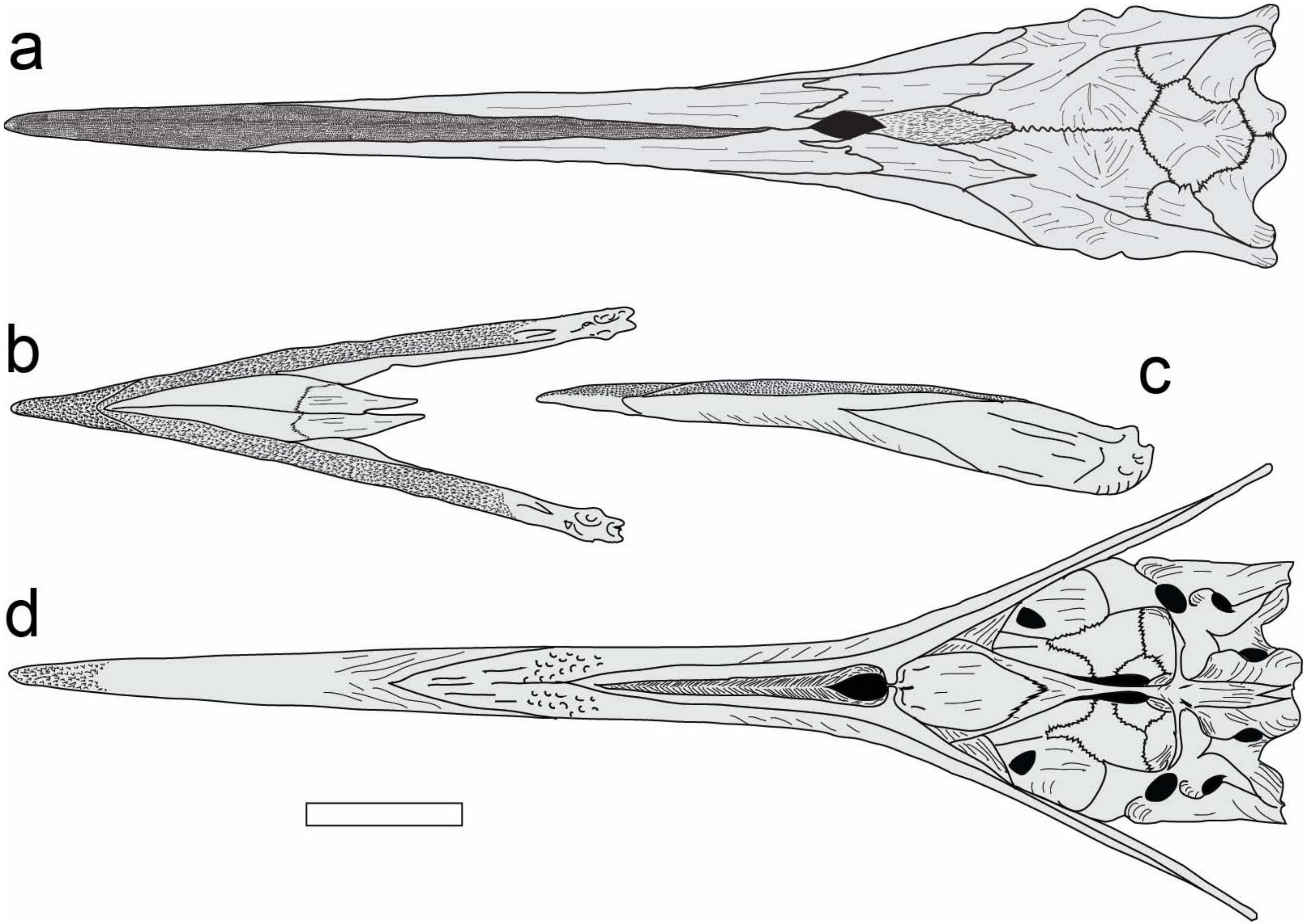

a
b
c
d

Figure 13. **a- h**; details of specific bones of the axial skeleton and appendicular skeleton of *Makaira* n. sp. 1; **a**, precaudal vertebrae 8 and 9 showing the rib socket; **b**, left articular in lateral view of the posterior region and the dorsal view of the joint for the quadrate; **c**, first left pectoral fin ray; **d**, caudal vertebra 15 showing it square shape in the neural spine and the lateral process of the vertebra; **e**, in situ second – dorsal fin with detail of the preserved pterigyophores and rays; **f**, articulated first anal – fin with details of the preserved pterigiophores and fin rays; **g**, transversal view of the caudal vertebra 13 in the second block at the level where the block was divided showing the lateral process; **h**, caudal peduncle showing details of the vertebrae 22 and 23. Abbreviations: Q-A = socket of quadrate – articular joint.

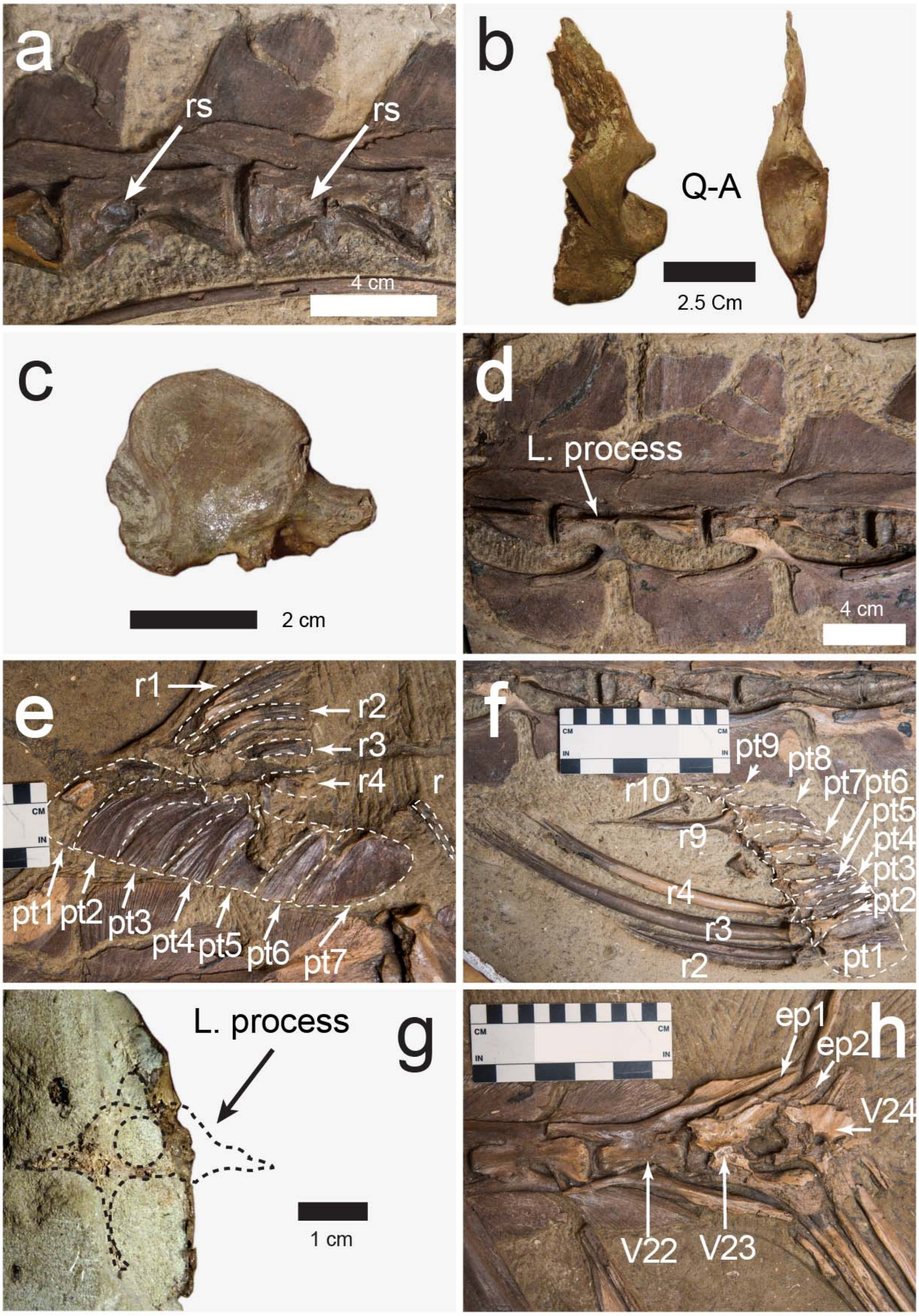
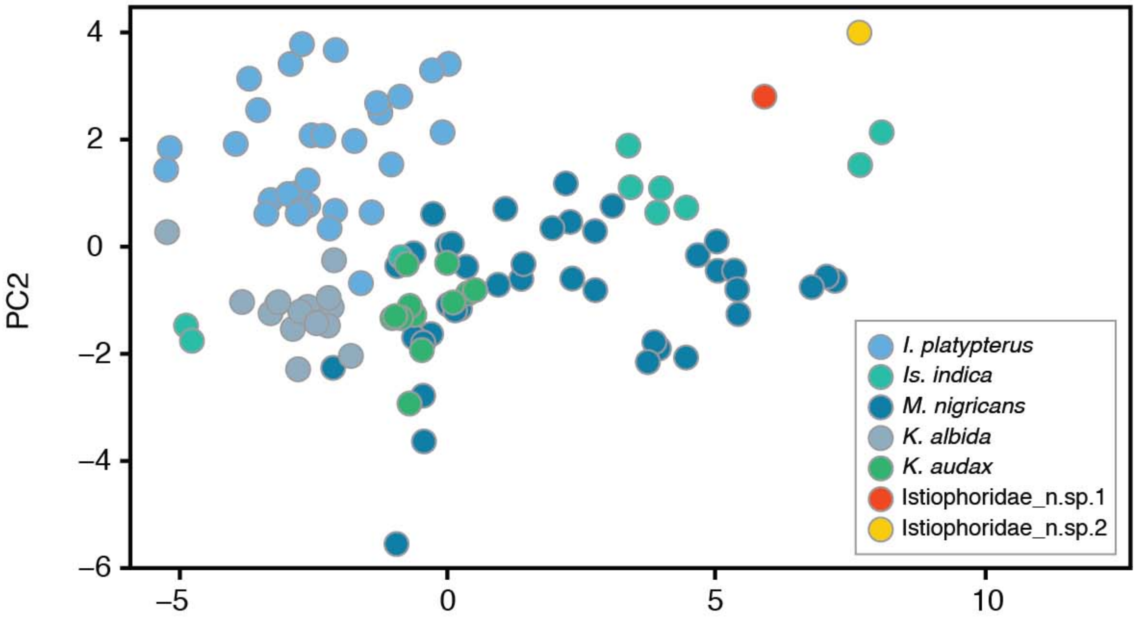

a
rs
rs
4 cm
b
Q-A
2.5 Cm
c
2 cm
d
L. process
4 cm
e
r1
r2
r3
r4
r
CM
IN
pt1
pt2
pt3
pt4
pt5
pt6
pt7
f
CM
IN
pt9
pt8
r10
pt7
pt6
pt5
r9
pt4
pt3
r4
pt2
r3
pt1
r2
L. process
g
1 cm
CM
IN
ep1
ep2
h
V24
V22
V23

Figure 14. **a**; PCA analysis with MAR imputed data for 18 rostral variables and 111 specimens distributed in 5 marlins species showing that the Chagres fossils are more or less close to *Is. indica*. The first two components explain the 78.1 % of the data variation in this analysis. **b**; PCA analysis for 5 articular variables of 81 specimens distributed in five modern marlin species and the specimen *Makaira*? n. sp. 1. The PCA analysis explains 95.2 % of the variation in the first two components. Both PCA support our descriptions and shows that Chagres specimens are more close to *Makaira* and *Istiompax* genera.

a


PC2
4
2
0
−2
−4
−6
−5
0
5
10
I. platypterus
Is. indica
M. nigricans
K. albida
K. audax
Istiophoridae_n.sp.1
Istiophoridae_n.sp.2

b

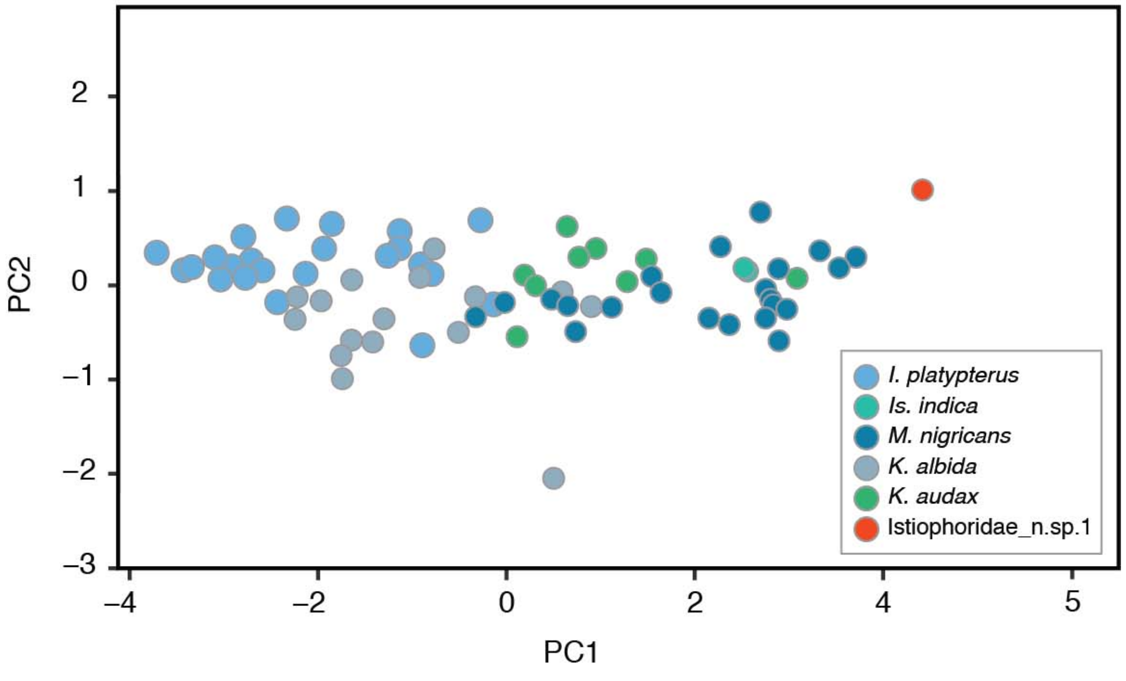

PC2
2
1
0
−1
−2
−3
−4
−2
0
2
4
5
PC1
I. platypterus
Is. indica
M. nigricans
K. albida
K. audax
Istiophoridae_n.sp.1

Figure 15. Boxplot comparing in a descriptive way selected ratios for dentary, vertebra 22 and 23 of modern marlins and Chagres specimens. The ratios for the dentary of the two Chagres specimens are more close to the group formed by *Kajikia* – *Istiophorus* indicating elongated lower jaw. For the vertebrae 22 and 23 the ratios of *Makaira*? n. sp. 1 are more close to the ratio of the spearfishes indicating a elongated vertebrae in the caudal peduncle.

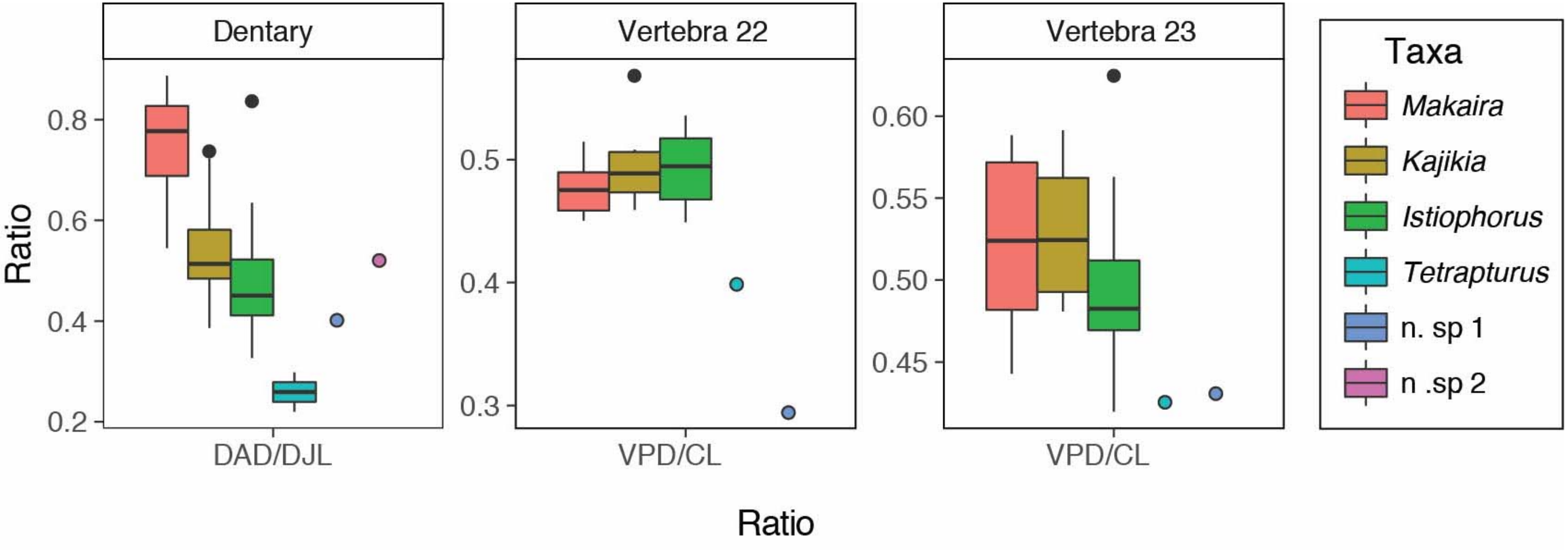
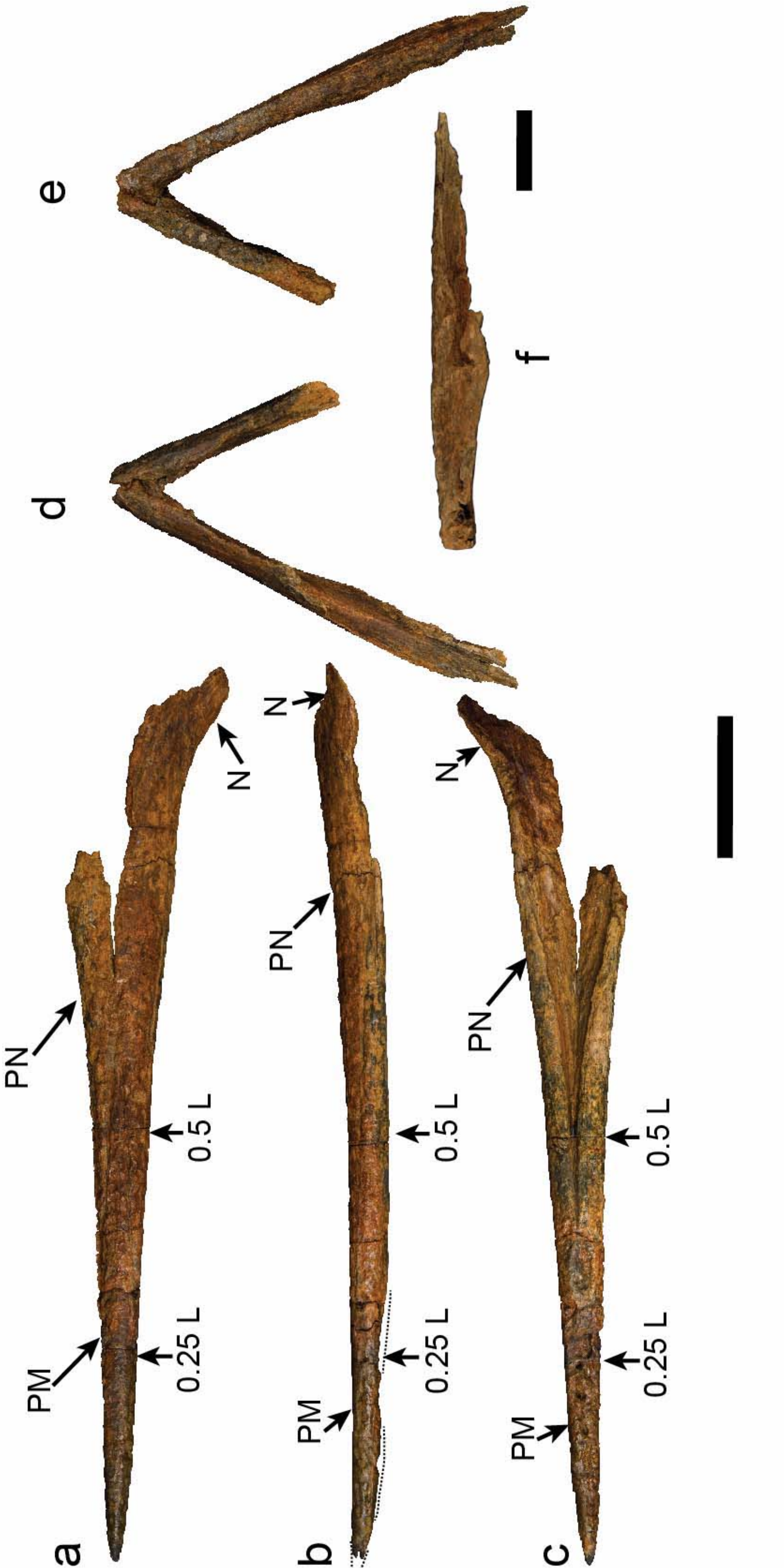

Dentary
Vertebra 22
Vertebra 23
Ratio
0.8
0.6
0.4
0.2
0.5
0.4
0.3
0.60
0.55
0.50
0.45
DAD/DJL
VPD/CL
VPD/CL
Ratio
Taxa
Makaira
Kajikia
Istiophorus
Tetrapturus
n. sp 1
n .sp 2

Figure 16. **a-f**; *Makaira* n. sp. 2 (STRI 31293); a, rostrum dorsal view; b, rostrum left lateral view; **c**, rostrum ventral view; **d**; articulate dentaries in ventral; **e**, articulate dentaries in dorsal view; disarticulated right partial dentary in lateral view showing the interdentary joint and the mandibular foramen. Missing bone is denoted by dash – lines. Scale bars: rostrum = 10 cm, lower jaw = 5 cm. See anatomical abbreviations for bone names.



a
PM
0.25 L
0.5 L
PN
N
b
PM
0.25 L
0.5 L
PN
N
c
PM
0.25 L
0.5 L
PN
N
d
e
f

Figure 17. Fossil Istiophorids - species rostrums in dorsal, right lateral and ventral view. **a**, *Makaira* gen. nov. *courcelli*; **b**, *Makaira belgicus*; **c**, *Makaira purdyi*. Scale bar = 5 cm.


a
TYPE
ORA 1478
b
c
481939

Figure 18. Cross - section of fossil istiophorids rostrums: **a – e**; *Makaira* gen. nov. *courcelli* (Arambourg, 1927); **a**, cross – section at the proximal end of the rostrum; **b**, cross section at 92 mm measured from its proximal end; **c**, cross – section at 139 mm measures from its proximal end; **d**, cross – section at 200 mm measured from its proximal end; **e**, cross – section at 260 mm measured from its proximal end; **f**, *Makaira belgicus* cross – section at the proximal end of the rostrum fragment; **g**; *Makaira purdyi* sketch of the computer tomography of at 0.25L distance (Fierstine 1999) **h**, *Makaira panamensis* cross – section approximately at 0.5L distance (Fierstine 1978), the prenasals sutures not showed by poorly preservation state; **i**, *Xiphiorhynchus solidus* cross – section at the proximal end of the rostrum. Scale bar = 1 cm.

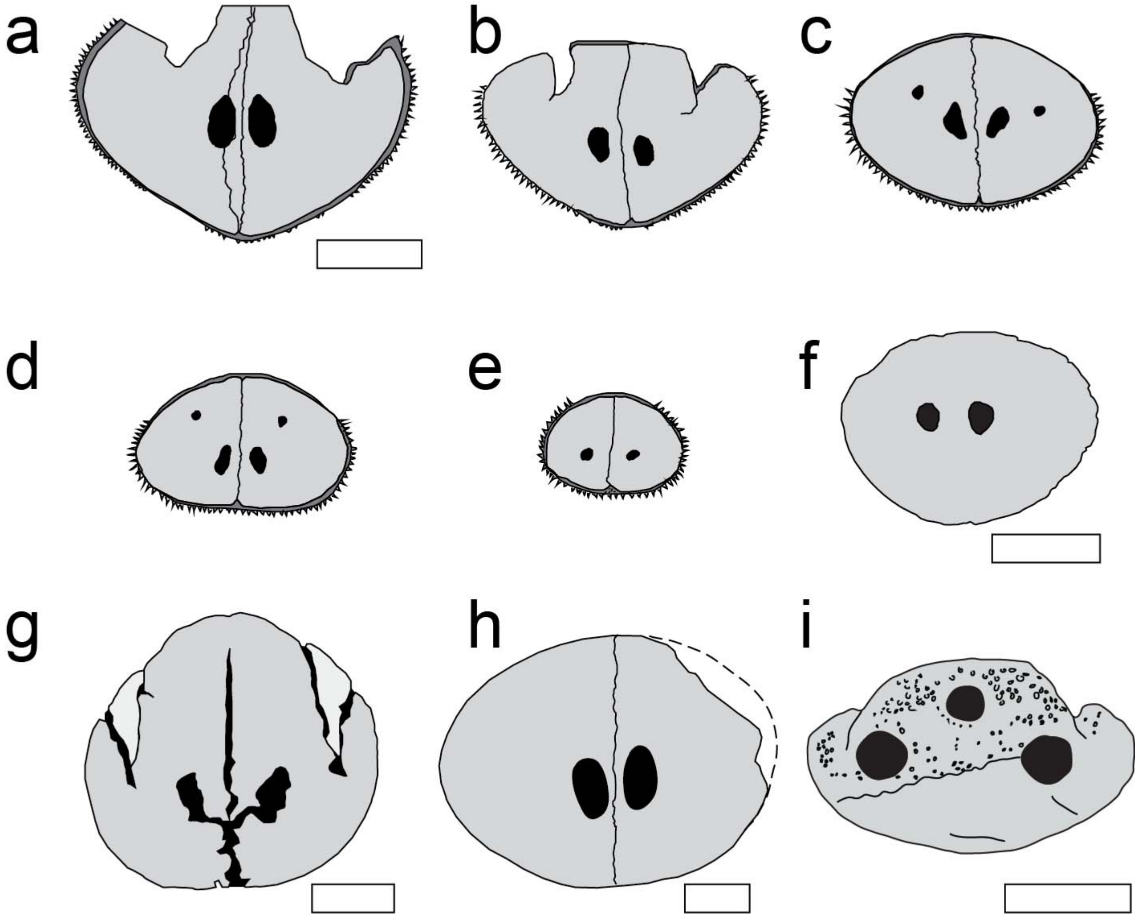

a
b
c
d
e
f
g
h
i

Figure 19. a- d; *Makaira panamensis* (USNM 18710, holotype, Late Miocene, Chagres sandstone, Caribbean coast of Panamá); **a**, skull dorsal view (scale bar = 20 cm); **b**, skull ventral view (scale bar = 20 cm); left lateral skull view (scale bar = 10 cm); **d**, occipital region view (scale bar = 4 cm).

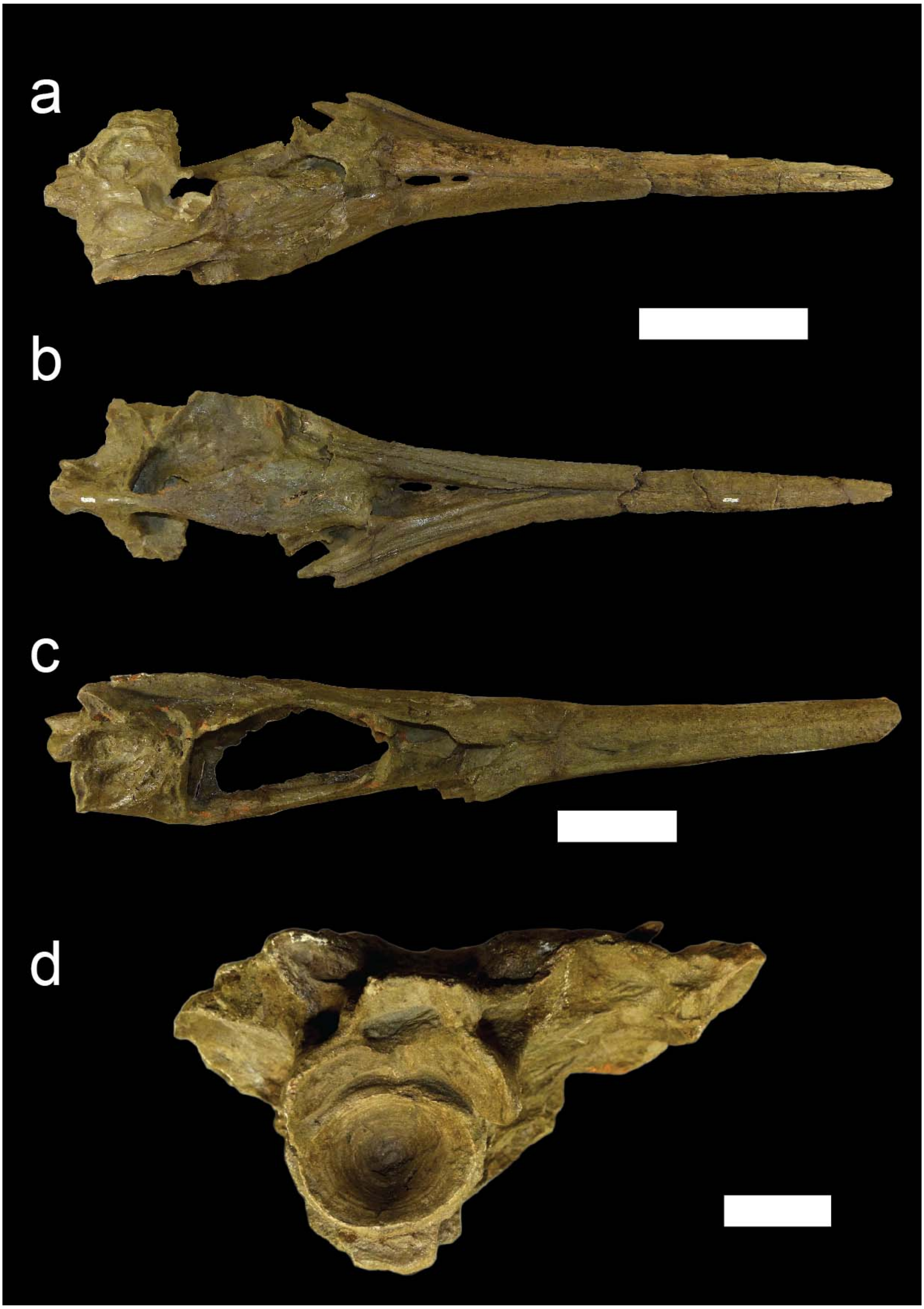

a
b
c
d

Figure 20. Missed specimen of *Makaira nigricans* misidentified like *Makaira teretirostris* (Rütimeyer, 1857). The picture represents the original diagram (Van Beneden, 1871) with the detail of the cross sections highlighted in computer to better observation.

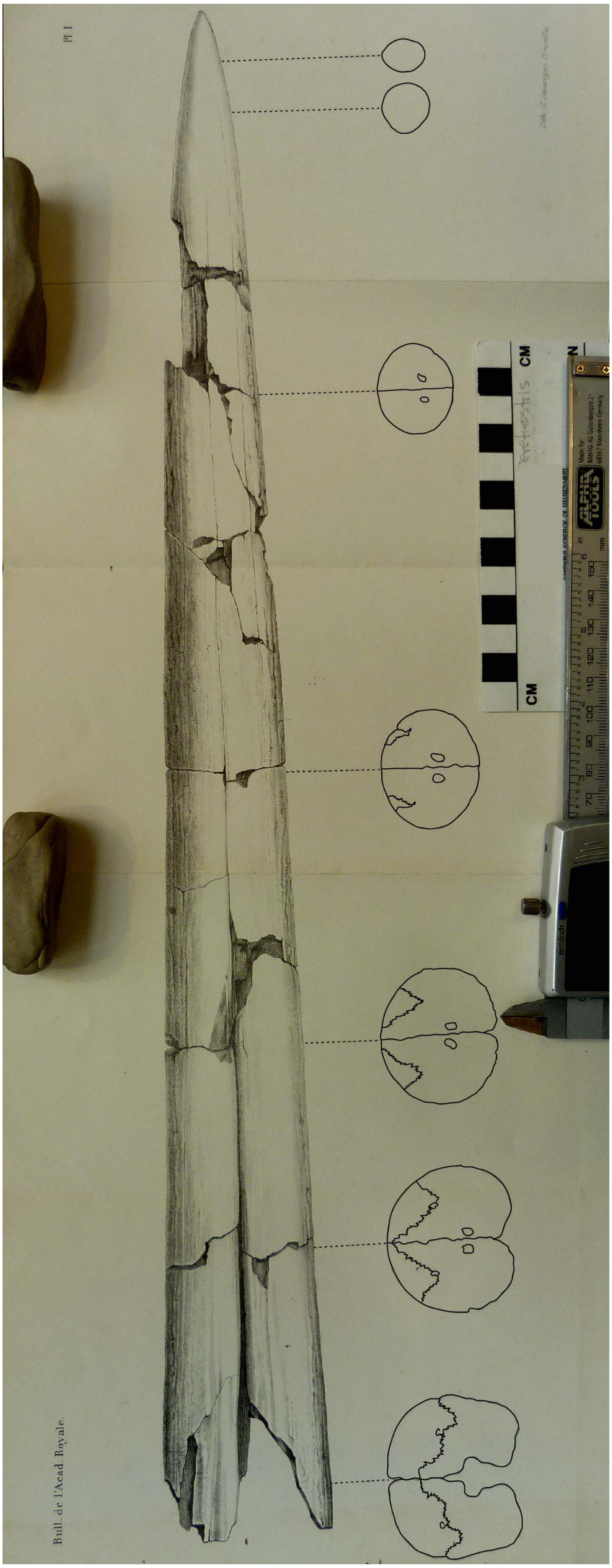

Bull. de l'Acad Royale.
Pl I
CM
CM

Figure 21. *Xiphiorhynchus solidus*; **a**, dorsal view; **b**, left lateral view; **c**, ventral view; **d**, cross-section of the posterior end; **e**, cross-section of the anterior end. The arrow indicates the position of the third nutrient canal.


d
e
a
b
c

Fossil marlins (family Istiophoridae) from the Piña locality (Panama; Chagres Formation; Miocene) – morphology and comparison with related forms

Fosilní mečouni (čeleď Istiophoridae) z lokality Piña (Panama; souvrství Chagres; Miocén) – morfologie a srovnání s příbuznými formami

Diploma thesis

SUPPLEMENTARY INFORMATION

Prague, 2017

SUPPLEMENTARY INFORMATION

Table S1. Rostral variables and its values for modern marlín species after data imputation. Observed values are entire values or values with one decimal number. Imputed values can be distinguied by having 9 decimal numbers. AR1 and AR2 variables were created after data imputation, NA indicates missed values.

Rostral variables and its measures for modern marlins species											
Number	**Species**	**L**	**D1**	**W1**	**H1**	**N1**	**DD1**	**IC1**	**D2**	**W2**	**H2**
LACM25302	*I.platypterus*	406.4	10	15.9	2	1.6	3.5	0.1	7.6	12.5	1.5
LACM25303	*I.platypterus*	406.4	11.2	16.1	2.3	2.8	3.7	0.7	8	12.1	1.5
LACM25306	*I.platypterus*	406.4	10	17.4	2.8	2.9	3.6	0.5	8.1	13.9	1.7
LACM25309	*I.platypterus*	419.1	10.1	13	2.1	1.5	3.6	0.1	7.8	11.4	1.232143781
LACM25311	*I.platypterus*	444.5	11.1	18.7	2.1	2.1	3.4	0.3	8.3	14.8	2
LACM25312	*I.platypterus*	464.8	10.7	17	3	2.2	3.1	0.2	8.1	12.1	1.825454006
LACM25314	*I.platypterus*	464.8	12.1	19.2	2.9	2.5	3.1	0.2	9.1	14.6	2.120003132
LACM25317	*I.platypterus*	508	12.4	19.5	2.8	2.5	5.1	0.8	9.5	14.5	2
LACM25318	*I.platypterus*	476.3	10.5	18.1	2.5	2.5	3.1	0.9	8	13.8	2
LACM25322	*I.platypterus*	426.7	10.3	17.3	3.6	2.4	3.2	0.3	7.7	14	2
LACM25325	*I.platypterus*	502.9	12.1	18.5	3	2.1	4.6	0.5	8.7	14.9	1.5
LACM25326	*I.platypterus*	533.4	13.3	20.9	3.3	2.5	4.6	1.2	10	16.1	1.9
LACM25485	*I.platypterus*	664	13.8	20.4	4.5	2.7	2.9	0.5	10.2	15.25494425	1.7
LACM25486	*I.platypterus*	496.5	12.4	17.9	3.2	2.6	4.3	0.5	8.9	14.5	2
LACM25487	*I.platypterus*	507.5	12.7	20.5	3	1.7	4.2	0.7	9	15.6	1.1
LACM25395	*I.platypterus*	503	14.5	21.9	2.1	2.1	5.9	0.5	10	17.5	1
LACM25425	*I.platypterus*	485	12.2	17.2	2.7	1.8	3.5	0.627927221	9.3	13.8	1.4
LACM25426	*I.platypterus*	515.5	11.7	16	3.1	1.6	3.1	0.605073055	8.4	11.8	1.129702952
LACM25427	*I.platypterus*	540.5	12.5	16	3.007088252	1.813311488	3.872254488	0.682178577	9.5	12.7	1.1
LACM25432	*I.platypterus*	506.5	12	16.5	2.3	2.3	4.9	0.9	8.5	12.8	1.4
LACM25434	*I.platypterus*	486.5	12.7	17.1	2.9	2.3	4.3	0.7	8.5	13.5	1
LACM25435	*I.platypterus*	503.5	11.1	15.9	2.9	1.5	2.9	1.1	8	11.6	1.2

LACM25436	*I.platypterus*	581	13.6	18.2	3.2	2	4.8	0.5	9.8	14.1	1.4
LACM25439	*I.platypterus*	551.5	12.4	17.3	2.9	1.7	4.1	0.8	8.8	11.8	1.1
LACM25443	*I.platypterus*	545	12.5	18.8	2.5	1.9	4.5	0.7	8.8	14.2	1.201649097
LACM25446	*I.platypterus*	513.5	12.4	16.7	2.699907288	1.867846691	4.042034357	0.663555495	8.7	13.3	1.1
LACM25447	*I.platypterus*	520	11.8	19.5	2.9	2.4	2.9	0.3	8.6	14.3	1
LACM25448	*I.platypterus*	570	12.8	19	2.9	2.9	4.6	0.7	9	13.5	2.4
LACM25449	*I.platypterus*	580	14	20.1	4.3	1.9	3.1	0.5	10	16.1	1.95084053
LACM25452	*I.platypterus*	565	13.6	18.4	3.094815852	2.070405559	4.588765841	0.799436349	10.5	15	1.1
LACM37998.001	*I.platypterus*	474.5	10.3	15.3	2.8	2.1	3.6	0.5	7.9	11.4	1.345949525
LACM 25316	*M.nigricans*	558.8	21.9	29.8	3.6	1.9	8.8	0.4	15.8	25.3	1.723921333
LACM 25321	*M.nigricans*	584.2	22.4	29.5	2.5	2	7.3	1.6	16	26.1	1.745717799
LACM 25329	*M.nigricans*	642.6	26.1	39	4	1.8	11.5	1.4	17	29.5	2.018526408
LACM 25330	*M.nigricans*	622.3	19	32.4	2.4	2	8	0.8	14.9	27.4	1.732591243
LACM 25331	*M.nigricans*	723.9	24.3	32.1	2.3	1.3	9.6	1.5	18.6	27.5	1.915134167
LACM 25480	*M.nigricans*	540	18.4	25.9	1.2	0.7	8.3	2.6	13.9	21.4	0.8
LACM 25481	*M.nigricans*	641	25.5	32.3	2.4	2.2	12.9	3.3	20.1	29.3	1.6
LACM 25484	*M.nigricans*	700	23.5	34.8	2.8	2.1	13	1.8	17.4	29.3	2.3
LACM 25457	*M.nigricans*	548	18.6	25.9	3.5	1.7	7.5	0.8	14.1	22	2.4
LACM 25458	*M.nigricans*	648	22.9	31.2	2.2	1.7	10.6	4	18.1	21.7	1.9
LACM 25459	*M.nigricans*	476	16.2	24.1	2.5	2	6.6	0.6	12.6	19.3	1.2
LACM 25460	*M.nigricans*	482	17.2	23.2	2.2	1.7	8.2	0.3	13.2	20.1	1.7
LACM 25474	*M.nigricans*	490	18.8	27.7	2.6	1.8	8.5	1.8	14.4	22	1.8
LACM 25475	*M.nigricans*	478	16.6	22.9	2.9	1.7	6	0.5	12.8	19.4	1.7
LACM 25476	*M.nigricans*	690	26.1	38.7	3.4	2.3	11.8	0.5	18.6	31.3	2
LACM 25477	*M.nigricans*	466	17.1	25.4	2.3	2.3	7	1.7	13.1	21.5	0.9
LACM 25488	*M.nigricans*	801	29.5	42.4	3.348455838	2.529400423	13.98544825	2.817499536	21.2	33.5	2.464463815
LACM 25489	*M.nigricans*	763	25.9	37.9	3.1	1.8	12.9	1.4	19.1	30	1.9
LACM 25491	*M.nigricans*	406	15.9	19.9	1.509165391	1.387748559	5.647177244	0.123017016	11	15.7	1.162972047
LACM 25492	*M.nigricans*	576	17.9	25	1.7	1.7	8.1	0.6	14.2	20	2.2
LACM 25463	*M.nigricans*	556	17.8	24.5	2.11707998	1.765082561	7.1	1.013586114	12.3	22.1	2.6
LACM 25473	*M.nigricans*	512.5	16.4	24.3	1.9	1.9	7	0.688104939	12.2	19.6	1.3
LACM 25464	*M.nigricans*	491.5	19.5	27.5	1.8	1.8	10.2	0.918649096	14.5	22.2	1.3
LACM 25456	*M.nigricans*	648	20.1	30.3	2.7	2.7	9.7	0.4	15.5	23.3	1.8

LACM 25403	*M.nigricans*	685	24.8	37.5	2.6	2.6	13.3	1.8	17.7	29.4	2.5
LACM 25404	*M.nigricans*	674	22.6	33.7	2.1	2.1	10	2.9	17.6	27.8	1.5
LACM 25406	*M.nigricans*	507	17.9	26.4	1.1	1.1	7.8	0.793916305	13.7	22.7	1.6
LACM 25407	*M.nigricans*	529	18.7	25.2	2.1	2.1	9	1	13.9	22.1	1.9
LACM 25409	*M.nigricans*	478	17.5	24.8	2.1	2.1	7.4	0.835843651	12.5	20.5	1.5
LACM 25410	*M.nigricans*	497	16.4	26.4	1.7	1.7	8.1	0.8	12.9	21	1.8
LACM 25411	*M.nigricans*	584	21.5	29.5	2.2	2.2	10.8	0.7	15.5	23.1	2.5
LACM 25412	*M.nigricans*	514	17.5	27.5	2.083564213	1.744279246	8.1	0.964486937	12.6	21.3	1.4
LACM 25413	*M.nigricans*	542	17.7	25.9	1.7	1.7	8.2	0.808336764	12.8	20.8	1.1
LACM 25414	*M.nigricans*	585	19.8	28.1	2.4	2.4	9.4	0.5	15.3	22.3	2
LACM 25415	*M.nigricans*	467	16.6	24	1.3	1.3	8.1	0.3	11.9	19.5	1.1
LACM 25416	*M.nigricans*	540	17.8	27.9	1.3	1.3	11.1	1.3	14.3	21.1	0.9
LACM 25417	*M.nigricans*	522	17.7	25.6	1.5	1.5	7.6	0.9	13	20.6	1.4
LACM 25418	*M.nigricans*	524	17.2	24.6	1.8	1.8	8.5	0.895198807	13	22.2	1.5
BRUUN 565-60	*M.nigricans*	805.5	27.1	39.8	3	3	13.6	4.3	20.6	31.3	2.5
VS 101	*M.nigricans*	692	27.6	37.2	2.91086596	2.257787367	12.00167076	2.176448919	19.5	29.9	2.154822875
USNM 196019	*M.nigricans*	750	30	42.2	3.21755374	2.448149187	13.39201442	2.625733513	22.7	33	2.37183679
LACM 25470	*Is.indica*	711	32.6	41.9	5.5	3.4	15.9	2.4	24.2	33.7	2.8
LACM 25509	*Is.indica*	607	24.2	32.4	4	3.2	10.4	3.3	18.5	27.5	2
LACM 25465	*Is.indica*	541	26	33.3	3.7	2.9	10.8	1.4	19.1	27.6	2
LACM 25466	*Is.indica*	502	22.7	29.5	4.6	3.1	9.5	1.5	18.9	24.5	2.2
LACM 25467	*Is.indica*	447	15	22.3	2.2	1.8	6.5	1.4	12.4	18	1.5
LACM 25468	*Is.indica*	556.5	21.2	30	3.878421417	2.811148478	10.33275176	2.036185301	16.4	23.9	2.104643643
LACM 25444	*Is.indica*	342.2	12.5	18.9	2.1	1.7	4.8	1.9	9.1	14.6	0.8
LACM 25445	*Is.indica*	340	12.4	18.9	1.8	1.9	5.1	1.5	9.3	15.9	0.8
MNHN2003.0420	*Is.indica*	655	22.53	32.58	4.000399276	2.874148431	10.6830072	2.068221358	16.57	25.24	2.182969243
MNHNA.5514	*Is.indica*	729.3800036	31.9223801	41.3811329	5.513220607	3.655500665	15.02702431	2.465546182	24.95	35.77	3.7
CAS3	*K.albida*	510	15.4	23.7	1.353481703	2.368778571	5.16638531	0.981568369	9.5	19.4	0.963279855
LACM25502	*K.albida*	446	13.4	21.9	2	1.8	5.5	0.5	9.9	19.2	1.2
LACM25503	*K.albida*	426	14.2	23.6	1.4	2.1	6.4	0.4	9.9	18.9	1.2
LACM25504	*K.albida*	496	12.9	20.1	1.8	2.1	4.5	1.3	9.4	17.7	1.1
LACM25505	*K.albida*	434	12.1	17.9	1.8	1.4	5.1	0.9	9.1	15.5	1.3
LACM25506	*K.albida*	478	13	20.6	1.8	1.9	4.9	1	10.3	16.9	1.3

LACM25400	*K.albida*	476	12.7	21.8	1.4	2	5.2	0.5	10.3	17.8	1.1
LACM25507	*K.albida*	435	2.7	19.5	1.914616975	1.425843904	5.531939493	0.542794021	9.4	17.8	1.374097774
LACM25401	*K.albida*	471	11	18.8	1.771775971	1.746478712	4.670271466	1.150099355	8.1	17.2	1.191405477
LACM25402	*K.albida*	439	13.4	21	1.2	2.1	5.3	1.1	9.7	17.4	0.9
USNM270768	*K.albida*	480	11	19.3	1.776357924	1.782453064	4.256796521	1.415055364	7.6	15.7	1.152434408
USNM270766	*K.albida*	465	13.9	22.4	1.646345146	1.895401944	5.178353495	0.8678715	8.7	16.7	1.159517091
USNM270769	*K.albida*	480	13.5	22.4	1.531344285	2.087995459	5.109677099	0.953770751	9.5	17.9	1.075957081
USNM270770	*K.albida*	450	11.4	20.3	1.769261062	1.735351091	4.815040838	1.057660234	8.6	15.9	1.204443957
VS100	*K.albida*	481.1808954	13.28890027	20.77341011	1.608883485	2.002589604	4.732120482	1.169164827	8.956920253	17.10870457	1.089219468
LACM 25483	*K.audax*	550	14.7	24	2.126380036	1.544822339	NA	1.817403088	9.6	18.5	1.365822196
LACM 25493	*K.audax*	525	15.7	23.3	1.6	1.4	NA	1.8	12.8	21	1.1
LACM 25494	*K.audax*	560.5	16.5	25.3	2.3	2.3	NA	2.1	12	19.6	1.4
LACM 25495	*K.audax*	554	16	23.6	1.9	1.7	NA	1	10.9	19.5	1.3
LACM 25496	*K.audax*	512	16.5	23.5	2.4	1.9	NA	1.7	11.5	19.6	1.6
LACM 25497	*K.audax*	518.5	16.3	20.3	2.4	1.6	NA	1.3	11.1	16.5	1.5
LACM 25498	*K.audax*	562.5	15	22.3	2.1	1.2	NA	1.7	11.3	18.6	1.3
LACM 25500	*K.audax*	656.5	20.1	26.7	3.5	2.3	NA	2	14.9	23.1	1.9
LACM 25501	*K.audax*	552.4746091	16.9551879	24.46338769	2.18379185	1.841700804	NA	1.341152154	12.33418661	20.07111563	1.399868368
LACM 25508	*K.audax*	689	23.9	33.5	3.2	2.9	NA	1.3	16.7	27.4	1.7
LACM 1	*K.audax*	550	18.6	25.8	2.236256657	2.002448155	NA	1.119452585	13.8	20.9	1.424599622
LACM 2	*K.audax*	527	13.8	23.6	1.993015055	1.572991885	NA	1.537357325	11.1	18.6	1.328168242
LACM 3	*K.audax*	543	14.7	21.4	1.933829989	1.574732572	NA	1.433860447	11.6	17.9	1.310836945
USMN 270773	*K.audax*	547	13.5	21.6	2.072692481	1.485635298	NA	1.840882142	10.7	17	1.346593158

Rostral variables and its measures for modern marlins species (continued)

Number	**Species**	**N2**	**DD2**	**IC2**	**P**	**VSPM**	**DVS**	**AR1**	**CA1**	**AR2**	**CA2**
LACM25302	*I.platypterus*	1	2.5	1	128	231	110	124.878308	3.141592654	74.61282552	1.767145868
LACM25303	*I.platypterus*	2	3.5	1	132	215	165	141.6229968	4.154756284	76.02654222	1.767145868
LACM25306	*I.platypterus*	1.5	3	1.5	122	134.5	140	136.6592804	6.157521601	88.42797922	2.269800692
LACM25309	*I.platypterus*	1	3	1.5	146	266	129.2032425	103.1227789	3.463605901	69.83760469	1.192374446

LACM25311	*I.platypterus*	2	3	2	139	249	163	163.0250968	3.463605901	96.47831039	3.141592654
LACM25312	*I.platypterus*	2	3	1.5	142	253.5	175	142.8639259	7.068583471	76.97687399	2.617168421
LACM25314	*I.platypterus*	2	2.5	1	151.8217703	263	209.6501242	182.4637013	6.605198554	104.348	3.529903935
LACM25317	*I.platypterus*	1.5	3	1.5	166.9362576	303	209	189.9092759	6.157521601	108.188597	3.141592654
LACM25318	*I.platypterus*	1	3.5	2	153	259.1409774	185.55203	149.264921	4.908738521	86.70795724	3.141592654
LACM25322	*I.platypterus*	1.5	3	1.5	141	242	213	139.9500987	10.1787602	84.66592201	3.141592654
LACM25325	*I.platypterus*	1.5	3.5	2	179.5	298	278.7	175.8113789	7.068583471	101.8111639	1.767145868
LACM25326	*I.platypterus*	1.5	4	2.5	188.6154257	298	289.4	218.3171275	8.552985999	126.4491043	2.83528737
LACM25485	*I.platypterus*	1.1	3.5	1	236.5	379.5	330.1263967	221.105291	15.90431281	122.208293	2.269800692
LACM25486	*I.platypterus*	1.3	3.4	3.1	165.0204687	276.5515486	219.2695688	174.3269763	8.042477193	101.355633	3.141592654
LACM25487	*I.platypterus*	1	3	2	179.9678389	311.5133298	233.3560338	204.4784118	7.068583471	110.2699021	0.950331778
LACM25395	*I.platypterus*	0.9	4.6	3.1	183.5529595	290.5	243.5	249.4031868	3.463605901	137.4446786	0.785398163
LACM25425	*I.platypterus*	0.8	3.8	2.4	120.5	269	140	164.8079506	5.725552611	100.7980003	1.5393804
LACM25426	*I.platypterus*	0.6	3.5	2.1	167.5	306.5	206.5	147.0265362	7.54767635	77.84866596	1.002347724
LACM25427	*I.platypterus*	0.671385869	3.455552684	2.117970151	186.1215349	332	245	157.0796327	7.102025534	94.75828841	0.950331778
LACM25432	*I.platypterus*	0.9	3.5	2.2	148	270.8981859	185.3822364	155.5088364	4.154756284	85.45132018	1.5393804
LACM25434	*I.platypterus*	0.8	3	2.1	166.5735486	293	180	170.5649191	6.605198554	90.12443925	0.785398163
LACM25435	*I.platypterus*	0.6	3.1	2.3	170.849348	314	195	138.6149219	6.605198554	72.88494956	1.130973355
LACM25436	*I.platypterus*	1.3	4.1	2.7	192.2060859	329.0801462	258.316643	194.4017534	8.042477193	108.5263182	1.5393804
LACM25439	*I.platypterus*	0.7	3.4	1.9	183.0952632	332	225	168.483614	6.605198554	81.55574529	0.950331778
LACM25443	*I.platypterus*	0.7	3.2	2.6	199	331.5	224	184.5685684	4.908738521	98.1433545	1.134083967
LACM25446	*I.platypterus*	0.75484995	3.446246099	2.200329102	180.5	310	170	162.6402517	5.725159412	90.87842149	0.950331778
LACM25447	*I.platypterus*	0.8	3.4	1.8	193.5	317	238	180.7201174	6.605198554	96.58826613	0.785398163
LACM25448	*I.platypterus*	0.8	3.5	1.6	196.5	340	244	191.0088333	6.605198554	95.42587685	4.523893421
LACM25449	*I.platypterus*	1.9	3.3	1	169	357	276	221.0110432	14.52201204	126.4491043	2.989051658
LACM25452	*I.platypterus*	0.823932422	3.845757658	2.50639266	198.8764246	320	295	196.5380364	7.522453412	123.7002107	0.950331778
LACM37998.001	*I.platypterus*	0.7	3	1.4	151.2276417	272.9777387	163.8586353	123.7708966	6.157521601	70.7329586	1.422811702
LACM 25316	*M.nigricans*	1.341837277	7.022391695	2.822112781	148	336	265	512.5665494	10.1787602	313.9550618	2.334128541
LACM 25321	*M.nigricans*	1.354896458	7.127090091	2.914906546	182	356	245	518.9911064	4.908738521	327.982273	2.393524964
LACM 25329	*M.nigricans*	1.518347575	8.437514587	4.076330466	173	381	330	799.4567905	12.56637061	393.8771789	3.200064652
LACM 25330	*M.nigricans*	1.347031785	7.06403724	2.859023059	186	287	321	483.4911094	4.523893421	320.6466542	2.357665083
LACM 25331	*M.nigricans*	1.456400933	7.940874375	3.636160259	192.5	463	265	612.6341294	4.154756284	401.7311606	2.880635379
LACM 25480	*M.nigricans*	0.8	6.7	3.7	158.5	308.3786426	262.8927705	374.2893487	1.130973355	233.6245377	0.502654825

LACM 25481	*M.nigricans*	1.1	11	5	234.5	380	359.5	646.8931973	4.523893421	462.5445404	2.010619298
LACM 25484	*M.nigricans*	2	9	4.5	213	432	396	642.298618	6.157521601	400.4116917	4.154756284
LACM 25457	*M.nigricans*	1.5	5.3	3.3	198	345.5	329.5	378.3577112	9.621127502	243.6305103	4.523893421
LACM 25458	*M.nigricans*	1.6	8.6	5.5	216.5	422	399	561.1512798	3.801327111	308.4808366	2.83528737
LACM 25459	*M.nigricans*	0.9	5.8	1.5	187.5	285	208	306.635151	4.908738521	190.9931254	1.130973355
LACM 25460	*M.nigricans*	1.5	6.4	2.4	148.5	305	272	313.4052831	3.801327111	208.3818407	2.269800692
LACM 25474	*M.nigricans*	1.1	6.3	3.5	158.5	297.5	272	409.0039476	5.309291585	248.8141382	2.544690049
LACM 25475	*M.nigricans*	1	5	1.9	148	302.5	269.5	298.5612578	6.605198554	195.0300719	2.269800692
LACM 25476	*M.nigricans*	1.6	8.9	3.6	217.5	427	375	793.3071229	9.079202769	457.2431028	3.141592654
LACM 25477	*M.nigricans*	0.9	6.2	3.1	151	284	234	341.1298383	4.154756284	221.2073927	0.636172512
LACM 25488	*M.nigricans*	1.785527441	10.57955587	5.974812972	224.5	543	518	982.3760228	8.806007121	557.7897756	4.770180066
LACM 25489	*M.nigricans*	1.4	9.5	5.7	224	501	447	770.9546912	7.54767635	450.0331476	2.83528737
LACM 25491	*M.nigricans*	1.005748954	4.327895769	0.43399196	112.5	228	124	248.5078329	1.788807288	135.6382628	1.062254143
LACM 25492	*M.nigricans*	1	7	2.2	184	343	334	351.4656781	2.269800692	223.0530784	3.801327111
LACM 25463	*M.nigricans*	1.7	4.4	1.4	163.5	346.5	322	342.5121391	3.520176278	213.4947828	5.309291585
LACM 25473	*M.nigricans*	1.2	5.7	0.7	143.5	309	270	312.9968761	2.83528737	187.8044088	1.327322896
LACM 25464	*M.nigricans*	1.7	3.2	2	153	293.1	265	421.1697651	2.544690049	252.8196688	1.327322896
LACM 25456	*M.nigricans*	2.2	6.4	2.9	218.5	434.5	408	478.3310435	5.725552611	283.6465467	2.544690049
LACM 25403	*M.nigricans*	1.5	9.1	4.5	228.5	460	430	730.420292	5.309291585	408.7054963	4.908738521
LACM 25404	*M.nigricans*	1.2	8	3.9	219.5	438.5	340	598.1749492	3.463605901	384.2796134	1.767145868
LACM 25406	*M.nigricans*	1.2	6.3	1.3	152	312	296	371.1477561	0.950331778	244.2509748	2.010619298
LACM 25407	*M.nigricans*	1.5	6.7	2.9	169	333.5	285	370.1110305	3.463605901	241.2664618	2.83528737
LACM 25409	*M.nigricans*	1.1	5.3	1.2	252.2	291	194	340.8628029	3.463605901	201.2582794	1.767145868
LACM 25410	*M.nigricans*	1.1	7.4	2.3	146.5	312.5918139	267.4910265	340.0459888	2.269800692	212.7643625	2.544690049
LACM 25411	*M.nigricans*	1.4	7.1	2.1	212.5	371.6667216	331.9653924	498.1387851	3.801327111	281.2118124	4.908738521
LACM 25412	*M.nigricans*	2	6.5	1	157.5	322.2938184	297.5	377.9728661	3.409601791	210.7851591	1.5393804
LACM 25413	*M.nigricans*	1	6.4	1	142.5	344.5	306.5	360.05008	2.269800692	209.104407	0.950331778
LACM 25414	*M.nigricans*	1.2	7.5	1.9	176.5	354.2004997	336	436.9798302	4.523893421	267.9699994	3.141592654
LACM 25415	*M.nigricans*	0.9	5.3	1.5	149	271	220	312.9026283	1.327322896	182.2516438	0.950331778
LACM 25416	*M.nigricans*	1.3	9.1	1.6	127.5	334	334	390.0444359	1.327322896	236.9781878	0.636172512
LACM 25417	*M.nigricans*	1.2	5	1.8	148	309	293	355.8796158	1.767145868	210.3296282	1.5393804
LACM 25418	*M.nigricans*	1.1	6.4	1.9	151	330	303	332.3176709	2.544690049	226.66591	1.767145868
BRUUN 565-60	*M.nigricans*	1.7	10.5	6.1	272.5	506.9400379	507	847.1147511	7.068583471	506.4090278	4.908738521

VS 101	*M.nigricans*	1.600008524	9.092208839	4.656583329	206.5	421	410.0590425	806.3840023	6.654789095	457.9263992	3.646809149
USNM 196019	*M.nigricans*	1.730030693	10.13462591	5.580473354	216	450	458.9848696	994.3140749	8.130953924	588.3417642	4.418343573
LACM 25470	*Is.indica*	2.1	12.4	4.1	217	361	340	1072.806767	23.75829444	640.5236182	6.157521601
LACM 25509	*Is.indica*	1.6	8.3	3.2	163.5	334	264	615.814992	12.56637061	399.5713156	3.141592654
LACM 25465	*Is.indica*	1.7	9	3.1	139.5	290	218	679.9977299	10.75210086	414.0304958	3.141592654
LACM 25466	*Is.indica*	1.8	8.6	2.7	138.5	240.1	199	525.9418801	16.61902514	363.6786196	3.801327111
LACM 25467	*Is.indica*	1.5	5.2	2.2	130.5	242.7	157	262.7156857	3.801327111	175.3008701	1.767145868
LACM 25468	*Is.indica*	1.556084716	8.136518078	3.066170274	168.5	312	245	499.5132319	11.8140791	307.8446641	3.478940693
LACM 25444	*Is.indica*	0.5	4.1	2	86	169.5	100	185.5503161	3.463605901	104.348	0.502654825
LACM 25445	*Is.indica*	0.5	3.6	2.6	94.5	174.4	83	184.0659136	2.544690049	116.1368264	0.502654825
MNHN2003.0420	*Is.indica*	1.605072105	8.392687973	3.124858306	155	293.6484222	236.3041586	576.5037718	12.56887947	328.4745606	3.742700842
MNHNA.5514	*Is.indica*	2.1	10.5	3.852732258	206.6731547	374.3909026	338.1540023	1037.498606	23.87264956	700.937623	10.75210086
CAS3	*K.albida*	1.075793878	4.498362252	3.216654011	130	275	260	286.6546217	1.438780886	144.7488815	0.728777301
LACM25502	*K.albida*	1.7	4	2.7	121	220	165	230.482945	3.141592654	149.2884829	1.130973355
LACM25503	*K.albida*	1.2	4.3	2.5	109.3650375	216	194	263.2026325	1.5393804	146.9558504	1.130973355
LACM25504	*K.albida*	0.8	3.6	3.5	150.3782267	280	246	203.6458898	2.544690049	130.6745464	0.950331778
LACM25505	*K.albida*	0.5	2.9	2.7	123.5	226.5	150	170.1093882	2.544690049	110.7804109	1.327322896
LACM25506	*K.albida*	0.8	4.1	3	119	269.5	198	210.3296282	2.544690049	136.7142583	1.327322896
LACM25400	*K.albida*	0.7	4.2	2.3	129.5	241	210	217.4453355	1.5393804	143.9948993	0.950331778
LACM25507	*K.albida*	0.897386624	3.291877869	2.377226309	102	213.601894	130.8046392	41.3512133	2.879079726	131.4128207	1.482945374
LACM25401	*K.albida*	0.619670277	3.379598536	3.129974199	139	266	183	162.4203402	2.465514132	109.4216721	1.114831075
LACM25402	*K.albida*	1	4.1	3.3	162	246	189	221.0110432	1.130973355	132.559502	0.636172512
USNM270768	*K.albida*	0.443130486	3.250869685	3.415203123	162	280	205.0121858	166.7400301	2.478282651	93.71370886	1.043091279
USNM270766	*K.albida*	0.907503984	3.817639725	2.903960688	105.5	250	193.9926347	244.5415722	2.128784289	114.1104992	1.055952032
USNM270769	*K.albida*	0.946691292	4.066682104	3.071618263	140	259.5725052	217.9210897	237.5044046	1.841770726	133.5569577	0.909242604
USNM270770	*K.albida*	0.682020822	3.426797455	3.031053612	125	271	185.0570734	181.756843	2.458519859	107.3953449	1.139365528
VS100	*K.albida*	0.742074547	3.777775465	3.25584979	157	269	217.9373794	216.8136988	2.033007913	120.3554375	0.931795634
LACM 25483	*K.audax*	0.928972497	4.853389251	3.937255219	155	315	200	277.088472	3.551171557	139.4867138	1.465136924
LACM 25493	*K.audax*	0.9	5.9	4.3	138.5	287	212	287.3065022	2.010619298	211.1150263	0.950331778
LACM 25494	*K.audax*	0.8	5.1	3.8	166.6	311.5	243	327.8644633	4.154756284	184.725648	1.5393804
LACM 25495	*K.audax*	1.3	5.1	2.5	130	297.5	255	296.5663465	2.83528737	166.9363796	1.327322896
LACM 25496	*K.audax*	1.3	4.7	3.3	130.5	289	185	304.5381379	4.523893421	177.028746	2.010619298
LACM 25497	*K.audax*	1	5.6	2.7	157	275	226	259.8803983	4.523893421	143.8456736	1.767145868

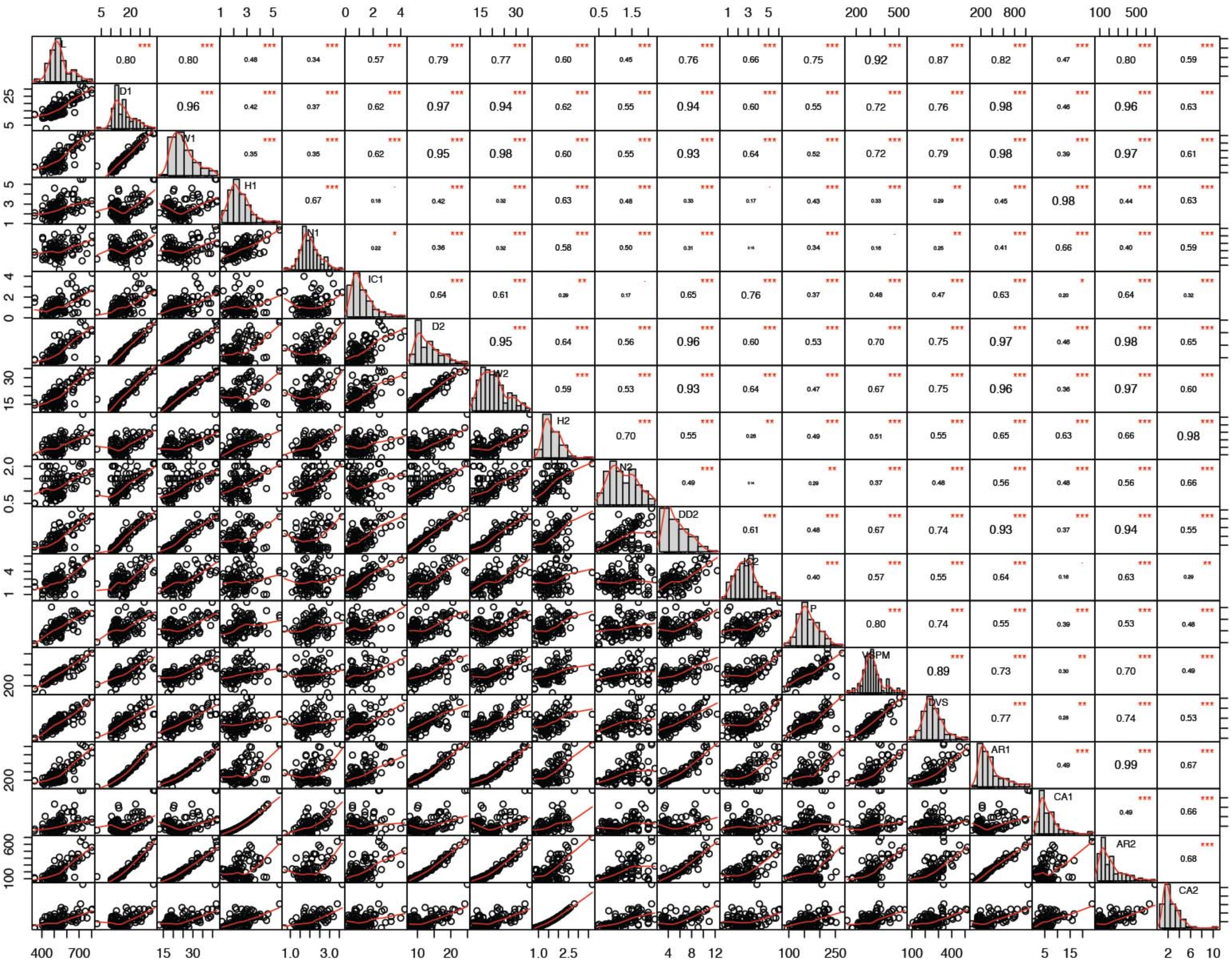
LACM 25498	*K.audax*	0.9	5.3	4.7	159.5	328.5	244	262.7156857	3.463605901	165.074986	1.327322896
LACM 25500	*K.audax*	1.5	6.3	4.9	175	371	290	421.4996324	9.621127502	270.3261939	2.83528737
LACM 25501	*K.audax*	1.196485427	5.865777367	3.157440722	120	315	222	325.7684986	3.745522092	194.4338649	1.53909094
LACM 25508	*K.audax*	1.6	9.2	4.1	146.6372706	346.8776341	315.5019526	628.8290395	8.042477193	359.3824916	2.269800692
LACM 1	*K.audax*	1.332143694	6.39447392	2.811884381	124.8412302	270	254	376.8968707	3.927653565	226.5245383	1.593953071
LACM 2	*K.audax*	1.014019278	5.075866808	3.365371064	140	289	215.9464839	255.7884739	3.119687122	162.1533048	1.385466613
LACM 3	*K.audax*	1.041171055	5.136009028	3.14730724	131	282	215.012421	247.0705542	2.937152275	163.0800746	1.349544557
USMN 270773	*K.audax*	0.893795975	4.690024363	3.941210752	153.5	316	212.1688358	229.0221044	3.374113016	142.8639259	1.424172804

Table S2. Articular measures and its values for modern marlins species. See methods and figure 6 c – d for description of measures abbreviations.

Articular						
Number	Species	ASM	AL	AW	ATW	AAL
AMNH27989SD	*I.platypterus*	10.9	6.9	5.9	9.5	6
AMNH27989SD	*I.platypterus*	11	7	5.6	9.2	5
AMNH27993SD	*I.platypterus*	9.8	6.5	4.6	8.5	6
AMNH27993SD	*I.platypterus*	11.5	8.5	4.5	8	6
AMNH39868SD	*I.platypterus*	10.3	6.8	5.2	8	5.5
AMNH39868SD	*I.platypterus*	9.5	7.6	5.3	8.5	5.5
AMNH57933SD	*I.platypterus*	8	6.2	4.4	6.8	5
AMNH57933SD	*I.platypterus*	8.7	7	5.5	7.6	5.5
AMNH57938SD	*I.platypterus*	8.7	6	5	7.1	5
AMNH57938SD	*I.platypterus*	10	6.2	5.5	7.3	5
AMNH79806SD	*I.platypterus*	9.4	5.9	4.9	7.2	5
AMNH94779SD	*I.platypterus*	10.5	6.6	4.9	6.9	5
AMNH94779SD	*I.platypterus*	10.2	7.4	5.5	7.4	5
LACM25325	*I.platypterus*	13.2	10.4	6	9.5	7
LACM25325	*I.platypterus*	13.4	9	7	9.3	7
LACM25326	*I.platypterus*	14	8.8	8.3	11.9	5.5
LACM25327	*I.platypterus*	13.3	9.5	6.9	8.8	6.5
LACM25395	*I.platypterus*	17.1	10	6.2	9.9	6
LACM25395	*I.platypterus*	14	10.7	7.1	10.4	6.5
LACM25485	*I.platypterus*	15.8	11.7	6.2	11.5	8
LACM25485	*I.platypterus*	16.4	11.1	8.5	11.9	6.5
STRI1628	*I.platypterus*	12.29	7.27	6.04	8.52	6.33
STRI1628	*I.platypterus*	12.5	7.99	5.88	7.9	6.68
AMNH56429SD	*K.albida*	10.5	6.2	8.3	11.8	6
AMNH57584SD	*K.albida*	10.9	6.5	8.3	12	5
AMNH57584SD	*K.albida*	10.8	7.8	7.6	10.9	5
AMNH57928SD	*K.albida*	11.5	6.7	6.6	9.1	5
AMNH57930SD	*K.albida*	12.5	7.5	8	10.9	6
AMNH57932SD	*K.albida*	14.8	9.8	9.4	11	7
AMNH57934SD	*K.albida*	11.6	10.1	7.6	10.8	7
AMNH7928SD	*K.albida*	12.6	9.1	7.8	10	5
ANMH56591SD	*K.albida*	11.5	8.8	6.5	9.5	6
ANMH57930SD	*K.albida*	14	10.3	8.8	12	6
ANMH57934SD	*K.albida*	11.5	10.1	7.5	10.9	8
USNM270766	*K.albida*	18.2	11.9	10.8	14.6	8
USNM270766	*K.albida*	16.4	12.2	10	13.5	8
USNM270768	*K.albida*	11.6	7.9	5.4	9.4	5
USNM270768	*K.albida*	11.6	9.3	6	8.9	5
USNM270775	*K.albida*	17.7	14.4	12.7	15.7	4
LACM25494	*K.audax*	17.7	13.9	7.6	13	9
LACM25494	*K.audax*	17.5	14.9	8.6	14	9
LACM25500	*K.audax*	18.8	13.3	9.9	16.4	9
LACM25500	*K.audax*	20.5	16.5	9.7	14.4	9
LACM25508	*K.audax*	23	18.7	14.4	20.6	12

USNM270773	*K.audax*	14.1	10.8	9.2	13.4	8.5
USNM270773	*K.audax*	13	11.5	9.6	15.2	7
USNM270774	*K.audax*	17.7	12	8.7	14.6	9
USNM270774	*K.audax*	16.8	11.8	8.4	13.6	7.5
LACM25509	*Is.indica*	21.8	18.6	13	17.6	10.9
LACM25509	*Is.indica*	20	18.9	13.1	17.8	11.3
AMNH28001SD	*M.nigricans*	19.9	14.9	14.2	20.9	10
AMNH28001SD	*M.nigricans*	19.5	16.8	15	20.5	12
AMNH57560SD	*M.nigricans*	21.5	14.1	15.2	22.3	12
AMNH57560SD	*M.nigricans*	23.8	18.7	16.2	23.3	15
AMNH57561SD	*M.nigricans*	23.4	18.5	16.3	22.2	14
AMNH57935SD	*M.nigricans*	16.3	10.7	10.1	14	8
AMNH57935SD	*M.nigricans*	16.4	14	10.7	14.2	7
AMNH88961SD	*M.nigricans*	17	14.8	11.9	15.5	10
AMNH88961SD	*M.nigricans*	16.3	14.8	12.6	16.7	10
AMNH88966SD	*M.nigricans*	18	15.4	14.5	18.8	10
AMNH88966SD	*M.nigricans*	20.4	15.6	12.6	16.8	12
AMNH90887SD	*M.nigricans*	18.7	16.6	15.5	22.5	12
AMNH90887SD	*M.nigricans*	19.8	18.5	15.1	20.8	10.5
BRUUN565-60	*M.nigricans*	23.3	20	14	21	13.5
BRUUN565-60	*M.nigricans*	22	18.4	14.8	21.7	10.9
HLF187	*M.nigricans*	18	14	10.7	15.1	8
HLF187	*M.nigricans*	16.5	11.3	10.1	15	8
LACM25419	*M.nigricans*	14.9	11.5	9	12.4	7
LACM25419	*M.nigricans*	15.1	12	8.2	11.7	6
LACM25484	*M.nigricans*	21.6	15.9	13.3	17	14.5
USMN196019	*M.nigricans*	23.2	17	12.2	22.3	12
USNM196019	*M.nigricans*	24.6	19	13.9	22.2	9

Figure S1. Matrix showing the behavior and correlation levels between 19 rostral variables used.


L
D1
W1
H1
N1
IC1
D2
W2
H2
N2
DD2
IC2
P
VSPM
DVS
AR1
CA1
AR2
CA2