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A new elasmobranch fauna from the early Miocene of Sharbithat (Sultanate of Oman) reveals the teeth of an ancient fantail stingray

Sylvain Adnet[1] and Vincent Charpentier[2]

[1]Institut des Sciences de l'Evolution de Montpellier (ISE-M)
UMR 5554 CNRS/UM/IRD/EPHE, CC064, Université de Montpellier, Montpellier, France.
E-mail: sylvain.adnet@umontpellier.fr, https://orcid.org/0000-0001-7188-1560

[2]Inrap, UMR 7041 CNRS, University of Nanterre
Nanterre, France. E-mail: vincent.charpentier@inrap.fr, https://orcid.org/0000-0002-8133-5931

ABSTRACT

Here we describe a new elasmobranch assemblage consisting of isolated dental material from the Aquitanian near-shore marine deposits of the Shuwayr and Warak formations at Sharbithat, in eastern Sultanate of Oman. The faunal composition clearly indicates affinities to other early Miocene elasmobranch-bearing localities worldwide. This assemblage is predominantly composed of large and common pelagic sharks as well as teeth attributable to a new species of fantail stingray, *Taeniurops tosii*, as old as the oldest undisputable fossil records of *Taeniurops*. The study of this fossil assemblage presented here improves the knowledge of the ancient elasmobranchs that frequented the eastern Arabian coasts during the closure of the Neotethys and the birth of the Arabian Sea.

KEYWORDS **Early Neogene. Elasmobranchs. *Taeniurops*. New species. Arabian Sea.**

INTRODUCTION

The mid-Miocene closure of the Neotethys (Terminal Tethyan Event, TTE) induced by the collision of the African-Arabian plate with the Eurasian plate is considered to be a major driver of tropical marine biodiversity (*e.g.* Cowman and Bellwood, 2013; Floeter *et al.,* 2008; Harzhauser *et al.,* 2007; Hou and Li, 2018; Liu *et al.,* 2018; Malaquias and Reid, 2009; Renema, *et al.,* 2008). The dynamics of the elasmobranchs that frequented the sub-basin of the Tethyan Seaway north of the Arabian Plate (Fig. 1, namely Mesopotamian Seaway [MS]) are however imperfectly understood. Although there are some records of early Miocene elasmobranch assemblages in western Neotethys (*e.g.* southern Europe), few are known easterly of the *Gomphotherium* land bridge connection that permitted terrestrial interchange between Eurasia and Africa since the late early Miocene (Harzhauser *et al.,* 2007). They include the Burdigalian elasmobranch fauna from the Moghra deposits, Egypt, (Cook *et al.,* 2010; Priem, 1920) and from Jabal Zaltan, Libya, (Argyriou *et al.,* 2015). With 15 sharks and rays recorded, these faunas represent the oldest eastern elasmobranch evidence in the eastern Palaeomediterranean Sea, Early Miocene elasmobranchs are unfortunately unknown from the MS deposits that have been affected by the collision between the Arabian and Eurasian plates and the simultaneous counterclockwise rotation of the Arabian plate (Bialik *et al.,* 2019; McQuarrie and Van Hinsbergen, 2013). More intriguing, early Miocene elasmobranchs are also unknown from the Paleo-Indian Ocean coasts are also unknown if we exclude some slinking reports in rare

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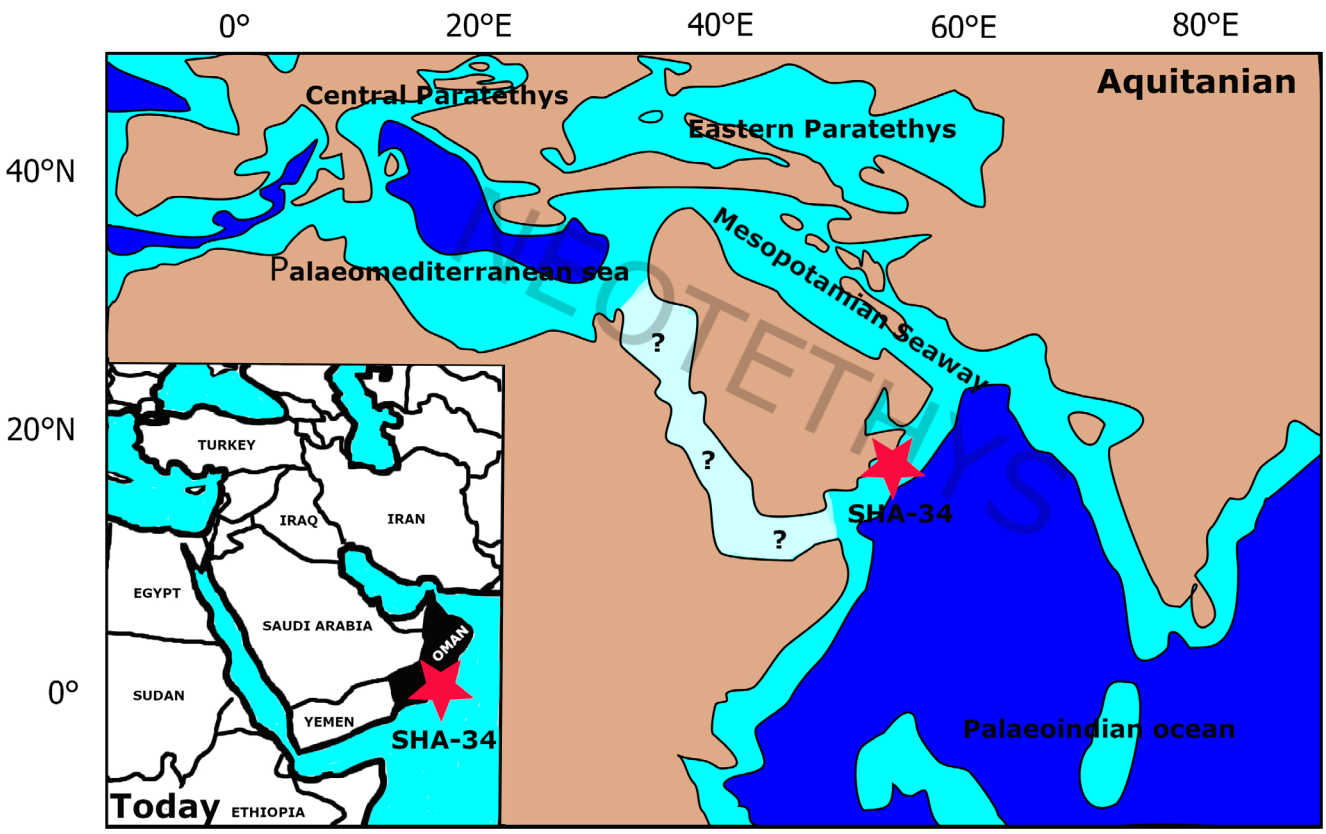

FIGURE 1. Location of the fossiliferous locality, SHA-34, eastern Sultanate of Oman (red star) in the present geography (left) and in the Aquitanian (22Ma) palaeogeography (right), after Bialik *et al.* (2019).

articles devoted to Middle East vertebrates (*e.g.* Roger *et al.,* 1994; Thomas *et al.,* 1989).

A fossiliferous early Miocene locality (named thereafter SHA-34) containing fossil fishes was retrieved at the Sharbithat Bay, eastern Sultanate of Oman (Fig. 1), some 4.6km to the east-northeast of the archaeological area where prehistoric collectors lost/left a damaged fossil tooth of *Otodus* (*Megaselachus*) cf. *chubutensis* 5,500 years ago (Charpentier *et al.,* 2020). This ancient human collecting, and transportation testify that the fossils outcropping in SHA-34 were already spotted by Neolithic maritime hunter-gatherers, at least as for the large teeth of the great mega-toothed shark *O.* (*Megaselachus*) cf. *chubutensis*. Charpentier *et al.,* (2020) identified a dozen of other fish species, including very well-preserved teeth of *O.* (*Megaselachus*) *chubutensis*, among the hundred specimens they collected at SHA-34. These remains include Hemigaleidae, Carcharhinidae, Sphyrnidae and Dasytidae and species of teleosts, such as Sphyraenidae, Labridae, and large Sparidae (Charpentier *et al.,* 2020, text only). The present report aims to illustrate and discuss some of these fossil elasmobranchs and precise the systematic affiliation of the batoid species belonging to Dasyatidae reported in Charpentier *et al.* (2020).

GEOLOGICAL SETTING

Neogen fossil vertebrates are quite unique for Sharbithat Bay, which is principally famous for its Neolithic relics and human heritage (Maiorano *et al.,* 2018). If geologists reported some fossils of invertebrates (*e.g.* Platel *et al.,* 1992b) and consisting of to date outcropping deposits in Sharbithat plain, none belonged to vertebrates. The SHA-34 locality (17°56'54.36"N – 56°13'36.18"E, see Charpentier *et al.,* 2020) is a low chalky spur belonging stratigraphically to the Shuwayr/Warak formations. In the Sharbithat area, including SHA-34, two stratigraphic formations crop out: the bioclastic limestones of the Shuwayr Formation (Fm.), and the Warak Fm. They are two successive local units belonging to Dhofar and Fars groups, respectively (Fournier *et al.,* 2004; Leroy *et al.,* 2012; Platel *et al.,* 1992b). Both formations, with a thickness ranging from 150 to 250m, account for most of the bioclastic limestones cropping out in the coastal plain of Sharbithat and extend westwards to Shuwaymiyah and onto the slopes of Wadi Warak. These well-bedded coral limestones of reefal bioclastic type are intercalated with debris flows rich in coral

fragments, echinoid spiculae and reworked foraminifera (Leroy *et al.,* 2012, fig. 14B; Platel *et al.,* 1992b), without any emergence and aerial exposure recorded in the Sharbithat plain (Pointu, 2007). Defined east of the Qarabiyan fault, the Shuwayr and Warack formations are cross-cut by major normal faults and considered as evidence of synsedimentary tectonics that dated the displacements along the faults to the late Oligocene or early Miocene (Fournier *et al.,* 2004; Leroy *et al.,* 2012; Platel *et al.,* 1992a). The sedimentary sequence in SHA-34 is unfortunately incomplete (Fig. 2A) leading to its unprecise stratigraphic position. Platel *et al.* (1992b) studied the sedimentology and invertebrate fossil assemblage of both formations in the Sharbithat area and reported that the highly diversified faunas were very similar and often concentrated in the interval of debris-flow beds. These faunas mainly consist of massive corals echinoids, lamellibranchs (see also Harzhauser, 2007), and foraminifers. The presence of *Schizaster* and *Eupatagus* in beds of white limestomes with brown flint (Fig. 2B) suggests that this level belongs to the top of the Shuwayr Fm. Nevertheless, the observed abundance of *Schizaster* in bioturbed chalky white limestone (Fig. 2B) reminds that found at the base of the Warak Fm. as reported by Platel *et al.* (1992b).

ELASMOBRANCH ASSEMBLAGE

The majority of the collected teeth exhibit typical abrasion by sand winds (levelling unpreferentially the enameloid crown and dentine root). In contrast, the tooth part that was embedded in the limestone is well preserved indicating minor post-mortem transportation. All specimens, grouped together as the "Sharbithat point 34" collection, are housed at the Department of Archaeology, Ministry of Heritage and Tourism of the Sultanate of Oman (reference MHT DA 52923) with the SHA-34 acronym (plus catalogue number).

Sharks

Otodus (*Megaselachus*) *chubutensis* (AMEGHINO, 1901) (Fig. 3A, B): A dozen teeth collected from the bioclastic chalky limestone at the SHA-34 locality (Fig. 2B). Some teeth from this locality are figured in Charpentier *et al.* (2020), and two are figured here (Fig. 3A-B). Considered as the ancestor (Perez *et al.,* 2019), of the famous mega-toothed shark *Otodus* (*Megaselachus*) *megalodon* AGASSIZ, 1843, *Otodus* (*Megaselachus*) *chubutensis* represents the largest toothed shark of early Miocene age that predate preferentially past marine mammals. Some indetermined pieces of ribs and of other bones recovered in SHA-34

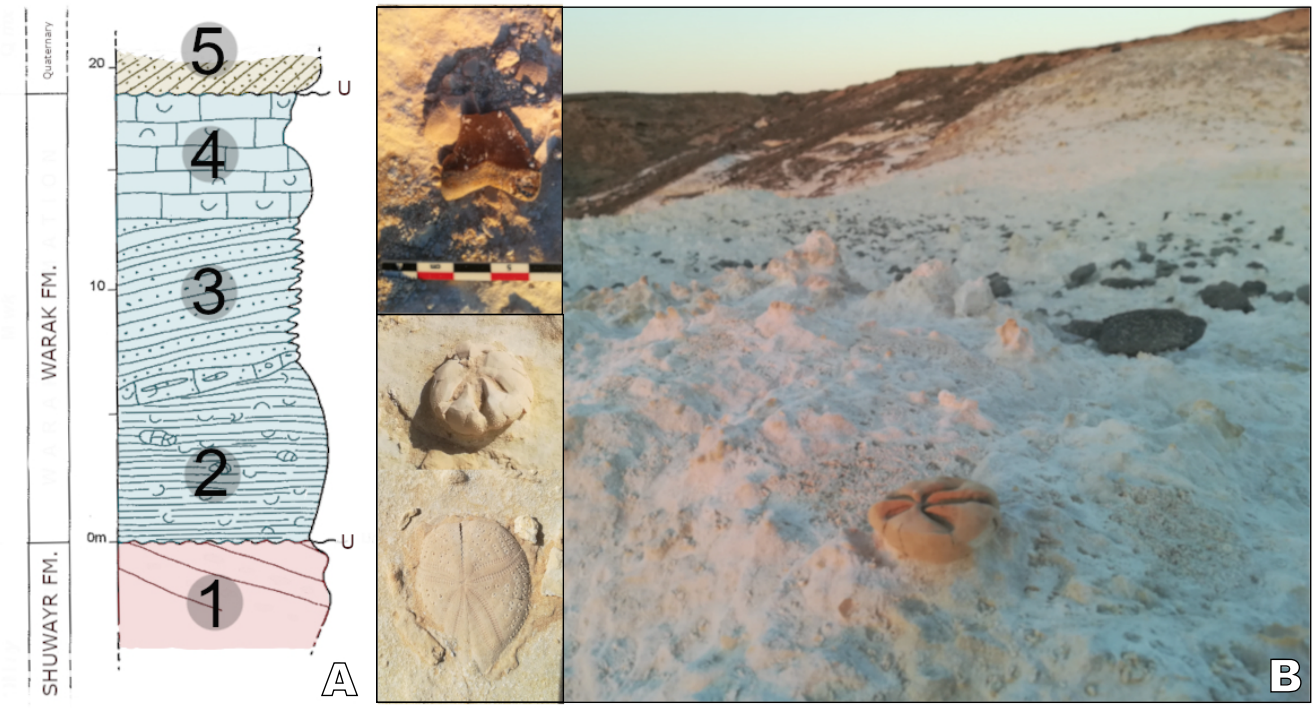

FIGURE 2. A) Sedimentologic log of Sharbithat plain modified after Platel *et al.* (1992b). 1: White chalky limestone with brown flint and echinoids; 2: Massive bedded yellow marly limestone with small blocks, oysters, other molluscs, corals, echinoids and foraminifera; 3: Alternating thin-bedded green to yellow marly siltstone and white biocalcarenite; 4: Yellow to white bioclastic limestone with molluscs and large foraminifera; 5: Ancient beach-rock. Abbreviation (U for Unconformity). B) SHA-34 locality and, at left from top to bottom: *Otodus* (*Megaselachus*) *chubutensis*, and the *echinoids Schizaster* and *Eupatagus*).

could indicate the occurrence of large marine mammals in the area and thus, possible ecological interaction between sharks and marine mammals. Contrary to the majority of large oceanic sharks that mainly hunt large bony fish, post Eocene species of *Otodus* (*Carcharocles*) and *Otodus* (*Megaselachus*) probably preferred food marine mammals which made a nutritious, high-calorie, scrumptious snack for its predators. As marine mammals doubled in size over the course of the late Paleogene and Neogene, *Otodus* (*Carcharocles*) and *O.* (*Megaselachus*), started to grow rapidly. However, Pimiento and Balk (2015) concluded that the body size of its youngest and famous representative, *O.* (*Megaselachus*) *megalodon*, seems to have been surprisingly stable during the Neogene. In fact, the increase in body size is relatively regular along chronospecies of *Otodus*, between *Otodus* (*Otodus*) *obliquus* (8m Total Length (TL)) and the giant *O.* (*Megaselachus*) *megalodon* (15m TL) (Shimada *et al.,* 2020). Maximum length of the body of *O.* (*Megaselachus*) *chubutensis* from Oman was deduced from linear regression following Shimada *et al.* (2020): TL(m)= 11.784cCH – 0.331 with cCH (mm) being the crown height of first/second anterior tooth. Total length of the largest Sharbithat specimen (Charpentier *et al.,* 2020, fig. 5B) is close to 6m, indicating that local representatives of this large predator were probably young individuals compared to contemporaneous adults that reached 10 meters long.

Isurus cf. *oxyrinchus* RAFINESQUE, 1810 (Fig. 3C, D): Two small (<1cm) teeth probably belonging to juvenile individuals. Unornamented crown, lack of numerous denticles and a massive root without trace of nutritive groove, relative minute size (less than 1cm), and presence of a pair of very tiny denticles in the upper tooth (Fig. 3D) are characteristics present in lamnid juvenile teeth. Crown and root morphologies are quite like those of figured Miocene representatives of *Isurus oxyrinchus (e.g.* Reneicke *et al.,* 2011: pl. 35-41), while the presence of tiny denticles remains intriguing compared to juvenile living specimens (Bemis *et al.,* 2015).

Galeocerdo aduncus AGASSIZ, 1843 (Fig. 3E–G): Compared to the coeval *Galeocerdo mayumbensis*, known in the Atlantic, the eastern Mediterranean (Argyriou *et al.,* 2015) and the south Indian Ocean (Andrianavalona *et al.,* 2015) during the early-middle Miocene period; the teeth of *G. aduncus* are smaller, have a more gracile crown with mesial cutting edge without any compound serration. These last features allow to distinguish the teeth of *G. aduncus* from those of the extant species *Galeocerdo cuvier* known from the mid Miocene. the morphology of *G. aduncus* teeth is closer to the morphology of the teeth of the small Paleogene *Galeocerdo latidens*. *Galeocerdo aduncus* is not an uncommon fossil tiger shark in early-middle Miocene deposits. It has been recorded in many localities, particularly in the Eastern Pacific, North Atlantic, Paratethys, and Mediterranean realms (*e.g.* Barthelt *et al.,* 1991; Bracher and Unger, 2007; Carrillo-Briceño *et al.,* 2020; Cappetta, 1970; Marsili *et al.,* 2007; Müller, 1999; Purdy, 1998; Purdy *et al.,* 2001; Probst, 1878; Reinecke *et al.,* 2011; Ward and Bonavia, 2001). The living tiger shark (*G. cuvier*) is a widespread shark that frequents all oceanic realms. Its Miocene fossil representatives (*G. aduncus* and *G. mayumbensis*) seem to have had the same ecological capability being collected in many coastal deposits around the world (Carrillo-Briceño *et al.,* 2019; Cappetta, 2012).

Hemipristis serra AGASSIZ, 1835 (Fig. 3H–J): The extinct snaggletooth shark species is very-well represented in worldwide Miocene deposits and its teeth became larger, though less numerous, in the Pliocene and until early Pleistocene in Gulf of Mexico (Ebersole *et al.,* 2017 and references herein). Distinction with its close and unique modern relative species *H. elongata* (KLUNZINGER, 1871) from the tropical shallow waters of the Indo-Pacific area is tenuous excepted its larger size (see Chandler *et al.,* 2006) and root histology (Jambura *et al.,* 2018).

Carcharhinus priscus (AGASSIZ, 1843) (Fig. 3K–P): As expected for this common fossil species, the upper teeth (Fig. 3K–M2) have a crown with a fine to triangular cusp with fully serrated cutting edges, serration being coarser on lateral heels than on median cusp where they decrease toward the top of the cusp. The crowns in the anterior teeth are more straight and larger (Fig. 3K) than those on the posterior teeth (Fig. 3M1, 2). The lower teeth (Fig. 3N-P2) have an unserrated crown, with a cusp more medially erected and distinct from mesial heel compared to upper teeth. The genus *Carcharhinus* includes 34 living species of "Requiem" sharks (*e.g.* Pollerspöck and Straube 2021) with many fossil representatives in Miocene deposits. Differences on tooth morphology between many living species of *Carcharhinus* are very tenuous (Naylor and Marcus, 1994; Soda *et al.,* 2017) and their use in taxonomy is complicated always having a blend of isolated teeth from several *Carcharhinus* species in Neogene deposits. However, few species occur in latest Paleogene – earliest Miocene. In addition to the most common and worldwide *C. priscus* (Cappetta, 2012), two other coeval species: *C. ackermanii* SANTOS AND TRAVASSOS, 1960 and *C. gibbesii* (WOODWARD, 1889) inhabited the Atlantic Ocean. However, both easily differ from *C. priscus* in having cusp of their upper teeth frequently unserrated (*e.g.* Aguilera *et al.,* 2017, fig. 3). With a global tooth morphology closer to the living copper and blacktip sharks (Reinecke *et al.,* 2011), *C. priscus* is usually reported in many early Miocene deposits from tropical to temperate latitudes.

Sphyrna laevissima (COPE, 1867) (Fig. 3Q1,2): Often incorrectly synonymised with the living species of the

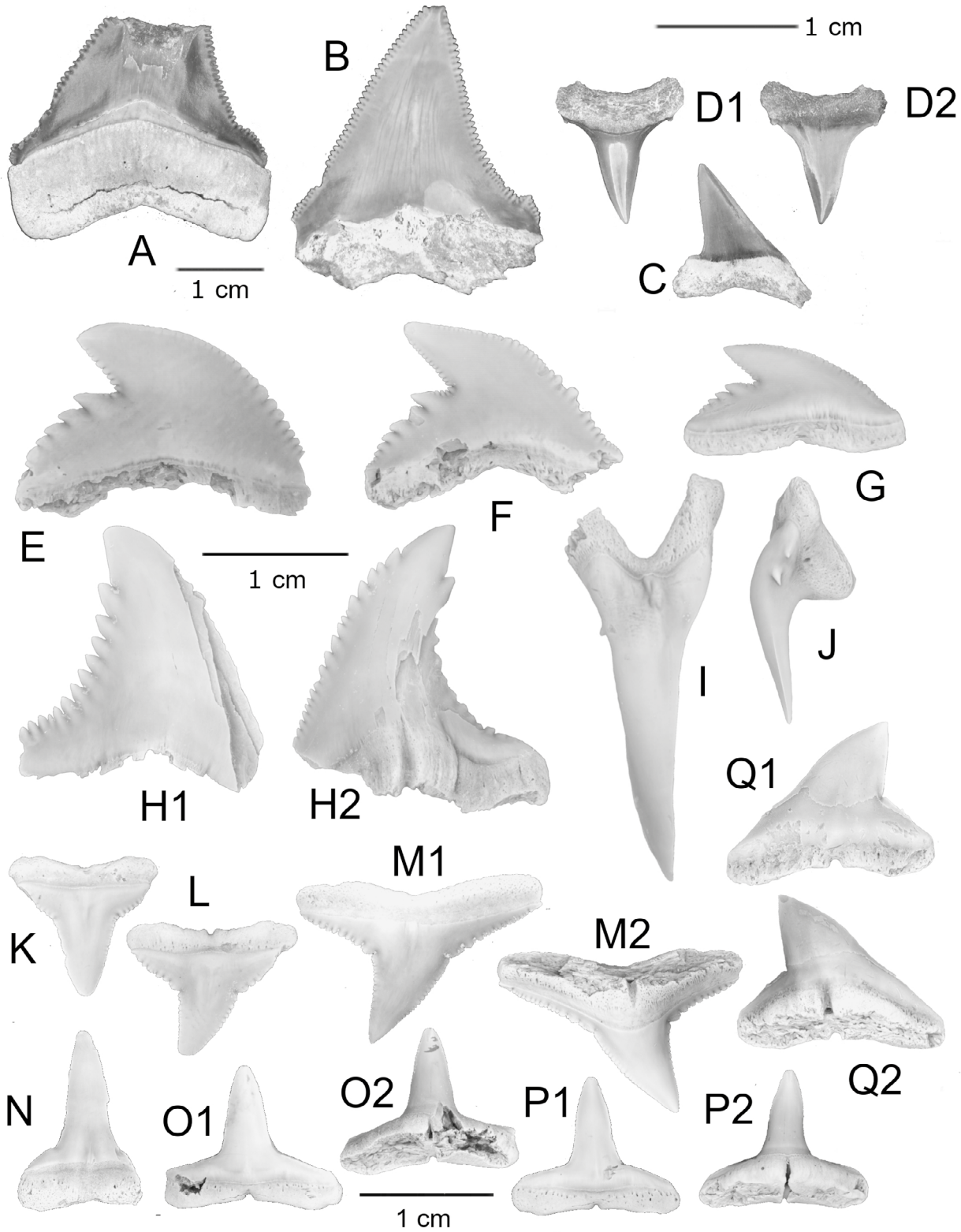

FIGURE 3. Sharks from SHA-34. A-B) *Otodus* (*Megaselachus*) *chubutensis*, A (SHA-34-4) antero-lateral tooth, lingual view, B (SHA-34-5) antero-lateral tooth, lingual view. C-D) *Isurus* cf. *oxyrinchus*, C (SHA-34-6) anterior upper tooth, C1 lingual and C2 labial views. D (SHA-34-7) lateral lower tooth, labial view. E–G) *Galeocerdo aduncus*, E (SHA-34-8), F (SHA-34-9), antero-lateral teeth, labial view, G (SHA-34-10) posterior tooth, labial view. H-J) *Hemipristis serra*, H (SHA-34-11) upper tooth; H1 labial and H2 lingual views; I (SHA-34-12) anterior lower tooth, labial view; J (SHA-34-13) lateral lower tooth in profile. K–P) *Carcharhinus priscus*, K (SHA-34-14) first anterior upper tooth, labial view; L (SHA-34-15) anterior upper tooth, labial view; M (SHA-34-16) lateral upper tooth, M1 labial and M2 lingual views; N (SHA-34-17) lower anterior tooth, labial view; O (SHA-34-18), P (SHA-34-19) lower lateral teeth, O1, P1 labial and O2, P2 lingual views. Q, *Sphyrna laevissima* (SHA-34-20), Q1 labial and Q2 lingual views.

hammer shark *Sphyrna zygaena* (LINNAEUS, 1758) (see Reinecke *et al.,* 2011 for a discussion). Teeth attributable to *S. laevissima* are frequently collected in late Oligocene to middle-?late Miocene coastal deposits of the Western and Eastern Atlantic Ocean and Eastern Pacific Ocean (see Carrillo-Briceño *et al.,* 2019; Kent, 2018).

Batoids

No macrofossil corresponding to usual large myliobatid teeth/spines nor pristid rostral denticles or vertebrae (sawfish) were collected in SHA-34. The unique fossil evidence of a batoid in SHA-34 are two dozen oral small teeth belonging to a unique Dasyatidae stingray (Charpentier *et al.,* 2020). These minute teeth look like those of the Miocene *Dasyatis cavernosa* (Probst, 1877), reassigned to the dasyatid genus *Taeniurops* by Bor *et al.* (2012).

Dasyatidae JORDAN AND GILBERT, 1879
subfamily Dasyatinae
Taeniurops GARMAN, 1913
Type species. *T. grabatus* (GEOFFROY SAINT HILAIRE, 1817) – living species
Taeniurops tosii nov. sp. (Fig. 4A-M)
Type material. Holotype (SHA-34-28) (Fig. 4H) is a lateral tooth of a possible male, whose cusp being few, erected and developed.
Type Locality and Age. SHA-34 (17°56'54.36" N - 56°13'36.18" E), Sharbithat area – Dhofar, Sultanate of Oman - top of Shuwayr Fm. (Dhofar Group) / base of Warak Fm. (Fars Group), Aquitanian in age.

Derivation nominis. Species name dedicated to Maurizio Tosi (1944-2017), full Professor at the University of Bologna (Italy), archaeologist and pioneer of maritime archaeology of ancient societies in the Indian Ocean. His main field of study was the formative processes of complex human societies.

Diagnosis. Teeth of medium size (up to 5mm width); crown cuspidated in anterior teeth of male and ovoid in female and lateral teeth of male. The crown has a distinctly hollowed labial face forming an oral depression bordered by a sinuous crest labially and by a regular transverse crest lingually. Enameloid of crown mainly smooth, except around labial crest. Lingual face trapezoid shaped, whereas its lingual visor being straight to undulating with median concavity. Root is quite wide and lingually extended in anterior rows with two lobes principally rounded and separated by a large nutritive groove in all tooth rows.

Description. In both male and female, tooth crown with a distinctly hollowed labial face forming an oral depression bordered by ornamented crests labially and by a smooth transverse crest lingually. Labial visor free of enameloid ornamentation and rounded in profile. Labial crest weakly developed in cuspidated teeth (Fig. 4A–D) to more salient in lateral male teeth and female teeth (Fig. 4I1). Irregular ridges of enameloid developed preferentially around labial crest of these lateral teeth (Fig. 4I2). In male with cuspidated teeth (Fig. 4A–D), the transverse crest weakly arching in profile (Fig. 4A2, D1), the cusp being quite strait. This cusp being triangular (anterior teeth) to very short and obtuse (lateral teeth) in oral view. Transverse crest sharp and rectilinear in females or non-mating males. Transverse crest devoid of any ornamentation of enameloid on all teeth. Lingual face entirely smooth and trapezoid shaped. Lingual visor straight (Fig. 4B, C, E) to undulating (Fig. 4G, H, L, M) in lingual view. When undulating, a median concavity is observed just over nutritive groove of root (*e.g.* Holotype, Fig. 4H). The root being as wider as crown and lingually extended in anterior tooth files (Fig. 4A–D) with two lobes, principally rounded and separated by a large nutritive groove in all tooth files. In basal view, one or two small nutrient foramens opening in groove. Labially, numerous small foramens visible under crown-root boundary (*e.g.* Fig. 4B2, D2, E2).

Discussion. Most of the subfamily Dasyatinae *sensu* Last *et al.* (2016) have jaws presenting sexual heterodonty with male teeth displaying a long, tapered cusp in all or some tooth files. Sexual dimorphism in *T. tosii* nov sp. seems light, as observed in the extant species of *Taeniurops* (Cappetta and Cavallo, 2006; Herman *et al.,* 1999). Morphologically, teeth of *Taeniurops* can be separated from those of other Dasyatinae (*e.g. Dasyatis*) by a crown having a distinctly hollowed labial face, the resulting depression being usually bordered by sharp crests labially and lingually (Cappetta, 2012). Moreover, the root lobes seem well-expended lingually and separated by a wider nutritive groove than in other Dasyatinae (*Dasyatis* genus included). Compared to the single fossil species of *Taeniurops*, *T. cavernosus* (Probst, 1877), the weakly arched transverse crest in profile and undulating lingual visor (with a median concavity) observed in the new species are different from the typical teeth of *T. cavernosus* (*e.g.* Bor *et al.,* 2012, plate 49). It instead resembles the Pliocene specimens *Taeniurops* aff. *grabatus* figured by Cappetta and Cavallo (2006). However, the new species easily separates from all described species by having an enameloid essentially smooth. Herman *et al.* (1999) and Cappetta (2012) figured teeth of the round fantail stingrays *Taeniurops grabatus* (Dasyatinae) but tooth illustration of the second living species *Taeniurops meyeni* (MÜLLER AND HENLE, 1841) was still unknown. Nevertheless, Cappetta and Cavallo (2006) reported that males of *T. meyeni* do not seem to have cuspidated teeth, in agreement with our own observations of some fresh specimens of *T. meyeni* (Fig. 4T–U) from the Indo-Pacific. Indeed, dental

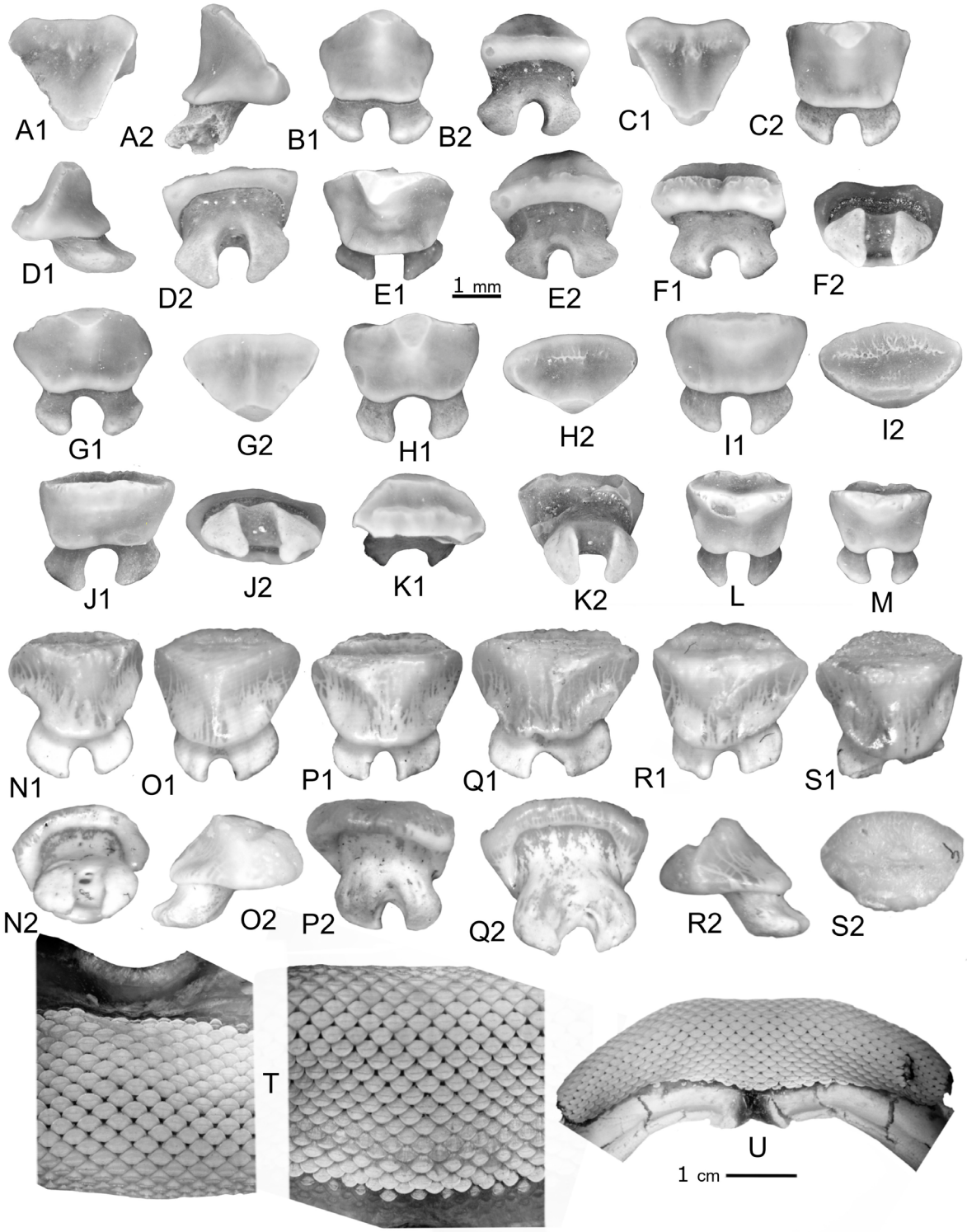

FIGURE 4. A1-M) *Taniurops tosii* nov. sp. A1-H2) male teeth from anterior (A) to lateral (H) files; I1-M. "female" teeth (or non-matting male teeth). A (SHA-34-21), A1 occlusal and A2 lateral views; B (SHA-34-22), B1 lingual and B2 labial views; C (SHA-34-23), C1 occlusal and C2 lingual views; D (SHA-34-24), D1 lateral and D2 labio-basal views; E (SHA-34-25), E1 lingual and E2 labial views; F (SHA-34-26), F1 labial and F2 basal views; G (SHA-34-27), G1 lingual and G2 occlusal views; H (SHA-34-28, Holotype), H1 lingual and H2 occlusal views; I (SHA-34-29), I1 lingual and I2 occlusal views; J (SHA-34-30), J1 lingual and J2 basal views; K (SHA-34-31), K1 labial and K2 basal views; L (SHA-34-32), lingual view; M (SHA-34-33), lingual view. N–T) *Taeniurops meyeni* (Collection from the Montpellier University, France: UM REC 1138M, Female, DW= 155cm) from Indian Ocean, N (Anterior lower tooth), N1 lingual and N2 basal views; O (anterior lower tooth), O1 lingual and O2 profile views; P (anterolateral lower tooth), P1 lingual and P2 labial views; Q (lateral tooth), Q1 lingual and Q2 labial views; R (lateral tooth), R1 lingual and R2 profile views; S (lateral tooth), S1 lingual and S2 occlusal views; T (jaws) symphyseal region of upper and lower jaws. U) *T. meyeni* (Collection from the Montpellier University, UM REC0815M, young Male, DW= 100cm) from Indonesia, lower jaw.

sexual dimorphism appears to be modestly pronounced in *T. meyeni* teeth, unless this reflected that all collected specimens were fished during the non-breeding period (Kajiura and Tricas, 1996). Surprisingly, teeth of *T. meyeni* do not resemble those of its sister species *T. grabatus*. Tooth morphology of *T. meyeni* is quite reminiscent of that of *Dasyatis* with *e.g.* lingual face of crown without strongly undulating visor (although undulating as in Fig. 4Q1). However, the root is well extended lingually (Fig. 4O2, R2), the nutritive groove opens widely in lingual view (Fig. 4T-S), and if enameloid of crown is lesser ornamented than in *T. grabatus*, it remains more than in *T. tosii* nov. sp.

The fossil teeth of *Taeniura* and *Taeniurops* have mostly been confused with those of the genus *Dasyatis*. Cappetta (2012) synthetized the dental difference between *Taeniura* and *Taeniurops*, considered as subgenus of *Taeniura* since Garman (1913) and until its resurrection by Last and Stevens (2009) for two valid living species, the Atlantic and Mediterranean *Taeniurops grabatus* and the Indo-Pacific *Taeniurops meyeni* (Last *et al.,* 2016; Naylor *et al.,* 2012). Cappetta (2012) also succinctly updated the fossil record of *Taeniurops* that now includes the Zanclean Mediterranean representatives of *T. grabatus* (Cappetta and Carvalho, 2006) and *T. cavernosus* from the Burdigalian of Bavaria, Germany. The latter (initially attributed to *Dasyatis* or *Taeniura*) is a common dasyatid taxa recovered in early-middle Miocene deposits from seas covering principally western and southern Europe (Bor *et al.,* 2012; Bracher and Unger, 2007; Cappetta, 1970; Probst, 1877; Reinecke *et al.,* 2008, 2011; Vialle *et al.,* 2011). The Aquitanian species *T. tosii* nov. sp. (this work) and the early Burdigalian *T. cavernosus* (Reinecke *et al.,* 2008) represent the oldest occurrence of the genus *Taeniurops*. Teeth of this coastal dasyatid genus are more frequently collected since middle-late Burdigalian, from Venezuela (Carrillo-Briceño, *et al.,* 2016) to south France and Germany (Bor *et al.,* 2012; Cappetta, 1970; Probst, 1877; Reinecke *et al.,* 2008, 2011). Principally affiliated to the extant species *T. grabatus*, the Late Miocene-Pliocene records seem to reflect the current distribution of living species because its fossils are known from Panama (Pimiento *et al.,* 2013), Portugal (Antunes *et al.,* 1999) to Italia (Cappetta and Cavallo 2006).

DISCUSSION

Concerning the paleoenvironemental inference, Platel *et al.* (1992b) suggested that the Warak Fm was deposited in the proximity of a N-S paleocanyon developed in a context of active local subsidence. Unfortunately, this small taxic association is irrelevant to conduct or support any paleoenvironmental consideration, as the main taxa are predominantly pelagic, with the possible exception of the new stingray.

Concerning the elasmobranch fossil record and dating interest, some previous paleontological studies reported fossil remains of sharks and rays in the Sultanate of Oman. Koot *et al.* (2013) described teeth, dermic denticules and fin spines of Ctenacantiforms and Hybodontiforms from the Middle Permian–Lower Triassic in the Haushi-Hugf region. Adnet *et al.* (2007) and Thomas *et al.* (1989) mentioned teeth of early Oligocene sharks and rays from Taqah and Thaytiniti, in the Dhofar region, and Roger *et al.* (1994) a rare spine remain of a ray from Ghaba in the early Miocene of the Dam Fm., in the region of Hugf. More broadly, Miocene elasmobranchs from the Arabian Plate are scarce and rarely illustrated. The only reported occurrences are *Galeocerdo* cf. *aduncus*, *Hemipristis serra*, *Carcharninus* aff. *priscus*, *C.* aff. *plumbeus*, *Scoliodon* sp., *Negaprion* aff. *eurybathrodon*, *Sphyrna* sp. *Dasyatis* sp. *Myliobatis* sp. *Aetobatis arcuatus*, and *Rhinoptera* sp. in the late lower Miocene of the Dam Fm., As-Sarrar, Saudi Arabia (Cappetta in Thomas *et al.,* 1982, unfigured), and *Dasyatis sensu lato* and *Pristis* sp. in the UAE (Otero, in press), and those previously detailed from Ghaba in the Sultanate of Oman.

All the fossil taxa from SHA-34 are consistent with an Aquitanian age, from earliest Aquitanian (top of the Shuwayr Formation) to latest Aquitanian (base of the Warack Formation). The Aquitanian large teeth of *O.* (*Megaselachus*) *chubutensis*, show all diagnostic features, such as crowns exhibiting triangular principal cusps with well-serrated cutting edges and separate lateral cusplets, at least in the smallest teeth, whereas the mesial ones seem to disappear completely in the largest specimen, prefiguring the evolutionary trend observed during the early-middle Miocene period and toward the youngest species *O.* (*Megaselachus*) *megalodon* in USA (Perez *et al.,* 2019). While this association of widely distributed sharks (*e.g. O.* (*Megaselachus*) *chubutensis*, *G. aduncus, H. serra, C. priscus, S. laevissima*) is relatively common in early Miocene (Middle East area included, see above), co-occurrence with the new species *T. tosii* nov. sp. is currently unique in tropical fossil elasmobranch faunas. Early Miocene elasmobranch faunas from the tropical belt westerly (*e.g.* Eastern Pacific, Atlantic, Central Paratethys and Mediterranean realms) are quite well-known *(e.g.* Argyriou *et al.,* 2015; Cappetta, 1970; Carrilo-Briceno *et al.,* 2016, 2019; Case, 1980; Cook *et al.,* 2010; Kent, 2018; Marsili *et al.,* 2007; Pimiento *et al.,* 2013; Purdy *et al.,* 1998; Suarez *et al.,* 2006). They display similar taxic associations of large pelagic sharks with *O.* (*Megaselachus*) *chubutensis*, *Isurus* spp. *Galeocerdo* spp., *Hemipristis serra*, *Carcharhinus* spp. as observed at Sharbithat, eastern Sultanate of Oman. Elasmobranchs from early Miocene deposits from the tropical belt easterly (*e.g.* Indian Ocean, Indo-Malaysian region and western Pacific) are lesser known. Numerous Indian palaeontologists of

the last century (*e.g.* Mehrotra *et al.,* 1973; Sahni and Mehrotra, 1981; Tewari, 1959) and more recently Patnaik *et al.* (2014) reported common faunal association from the early Miocene of Kutch, India (*e.g. O.* (*Megaselachus*) *chubutensis*, *Galeocerdo* spp., *Hemipristis serra*, and *Carcharhinus* sp.) but no fossil could be currently compared with the new *Taeniurops* species. Welcomme *et al.* (1997) also reported a Burdigalian fauna from Baluchistan, Pakistan (*e.g. Carcharhinus*, *Galeocerdo*, *Hemipristis*, *Sphyrna*) with the presence of a stingray, *Dasyatis* sp., but the latter material is too fragmentary to compare with our material. Southerly, Priem (1907) and Andrianavalona *et al.* (2015) also reported elasmobranch associations from the Miocene of the Mahajanga Basin, northwestern Madagascar, with quite similar association of sharks with *O.* (*Megaselachus*), *Carcharhinus*, *Galeocerdo*, *Sphyrna*, *Hemipristis* and stingrays. Presence of *C. priscus* and *G. mayumbensis* would suggest an early to middle Miocene age according to the last authors. However, occurrence of *O.* (*Megaselachus*) *megalodon* in the Miocene of Mahajanga Basin suggests that the fauna at SHA-34 is somewhat oldest than those from northwestern Madagascar. Knowledge of early Miocene elasmobranchs from Indo-Malaysian region are mainly based on old literature (*e.g.* de Beaufort, 1926; Martin, 1883-1887; Noetling, 1901) and unprecise dating. One can suspect that some taxa reported by Leriche (1954) as *O.* (*Megaselachus*) *megalodon var. indica* from Java, Indonesia, are conspecific with *O.* (*Megaselachus*) *chubutensis* but most of these reports require revisions as recently performed by Marramà *et al.* (2018) on a holomorphic stingray from the early Miocene of Sulawesi, Indonesia. The tooth morphology of the revised *Protohimantura* Marrama *et al.* (2018) is consistent with that of *Himantura* and by this, clearly different from *Taeniurops tosii* nov. sp.

CONCLUSION

Bialik *et al.* (2019) and Torfstein and Steinberg (2020) have recently updated the timing (late Oligocene–middle Miocene) and tempo of closure of the MS that resulted from the northward movement of the African–Arabian plates. Bialik *et al.* (2019) pointed out that water mass exchange between the Mediterranean Sea and Indian Ocean via the MS was strongly reduced at ca. 19.7Ma, at least 6Ma before the terminal closure of the seaway (at 13.8Ma) that coincides with *Gomphotherium* land bridge event. A second marine connection between both oceanic realms across the Red Sea may still have existed (Segev *et al.,* 2017), until at least the Aquitanian (Fig. 1). However, the feasibility and evolution of significant exchange of water masses between the Mediterranean Sea and Indo-Pacific oceans by the putative Red Sea Gateway is still debated (Bialik *et al.,* 2019; Torfstein and Steinberg, 2020). The elasmobranch fauna from the Sultanate of Oman may illustrate what the fauna living in the new north-western extremity of the Indian Ocean (prefiguring the Arabian sea fauna) looked like. This fauna includes most of the pelagic sharks that dwelled in the early Miocene tropical seas plus a new fantail stingray *Taneiurops tosii* nov. sp. The latter species, as old as the coeval fantail stingray species *T. cavernosus* known as far as western Mediterranean, could indicate that splitting of the two *Taneiurops* lineages was before the beginning of the Neotethys closure. This clearly supports the assumption of a reduced water mass exchange between Indian Ocean and Mediterranean Sea even earlier than earliest Miocene. If both living species of fantail stingrays could result from such dispersal and vicariance processes, it would support the hypothesis that Neotethys closure played a main role in establishment of modern tropical marine biodiversity.

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