Rupelian Fossil Elasmobranch from Omani Thaytiniti Fauna Fill A Chronological Gap in The Elasmobranch Fossil Record of West Indian Ocean

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ABSTRACT

In 1990's, French-Omani team first signalled in southern part of Dhofar, South Oman, several terrestrial vertebrates mixed with marine members in an Early Oligocene fossil assemblage. Even though most of these fossils have been reported and published by palaeontologists, fossil elasmobranchs (sharks and rays) have deserved little attention since this date. In this paper we describe and figurate the elasmobranch members recovered during the 90's fieldtrips at Thaytiniti and which includes several requiem sharks (*Carcharhinus perseus; Negaprion, Rhizoprionon*), snaggletooth shark (*Hemipristis, Moerigaleus*), nurse and zebra shark (*Nebrius, cf. Stegostoma*); bamboo shark (*Chiloscyllium*), tiger shark (*Galeocerdo*); wedgefish and guitarfish (*Rhynchobatus; Rhinobatos*) and several stingrays (e.g. *Himantura,?Taeniura*), cownose and eagle rays (*Rhinoptera, Aetobatus*). Together with the fossiliferous outcrops at Paali Nala, Pakistan, the Oman locality Thaytiniti fill the chronological gap in the fossil record of West Indian Ocean elasmobranch communities. Their resembling elasmobranch assemblages constitute an original and significant amount of new elements about the Late Paleogene tropical ichtyofauna living close to estuaries and support that the settlement of the modern Indian Ocean fish fauna occur during Early Oligocene to Early Miocene period as these sites interestingly mostly present members known in present Indian Ocean.

KEYWORDS: Oligocene, Elasmobranches, Indo-Pacific

أحفورة الروبيلي من حيوانات موقع ثايتينيتي العُماني تملأ فجوة زمنية في السجل الأحفوري للأسماك صفيحية الخياشيم الغضروفية لغرب المحيط الهندي

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الملخص:

في تسعينيات القرن الماضي، أشار فريق فرنسي عماني لأول مرة في الجزء الجنوبي من ظفار بجنوب سلطنة عمان، إلى وجود العديد من الفقاريات الأرضية الممزوجة بأعضاء بحرية في تجمع أحفوري من فترة الأوليجوسيني المبكرة، في حين تم الإبلاغ عن معظم هذه الأحفوريات ونشرها من قبل علماء الأحفوريات، إلا أن أحفوريات الأسماك صفيحية الخياشيم الغضروفية (أسماك القرش والشفنين) لم تجد سوى القليل من الاهتمام حتى الآن. نقوم في هذه الورقة بوصف وتصوير أعضاء هذه الأحفوريات المكتشفة خلال الرحلات الميدانية في التسعينات من القرن الماضي في قرية ثايتينيتي (بالقرب من منطقة عيدم في أقصى جنوب غرب محافظة ظفار)، والتي تتضمن العديد من أسماك قرش القداس، والقرش ذو الأسنان المسننة، والقرش الحاضن، وقرش الحمار الوحشي، وقرش الخيزران، وقرش النمر، وقيثارات البحر، وسمك السلفوح، والعديد من سمك الشفنين اللساع، والشفنين خطم البقرة، والشفنين العقابي. جنبا إلى جنب مع التكشفات الأحفورية في بالي نالا بباكستان، يملأ موقع ثايتينيتي في سلطنة عُمان الفجوة الزمنية في السجل الأحفوري لمجموعات الأسماك صفيحية الخياشيم الغضروفـة من غرب المحيط الهندي. تشكل مجموعاتها المشابهة من الأسماك صفيحية الخياشيم الغضروفية كمية أصلية ومهمة من العناصر الجديدة حول الإكتيوفونا (مجموع أنواع الأسماك الأصلية الخاصة بالمنطقة) الاستوائية من العصر الباليوجيني المتأخر التي تعيش بالقرب من مصبات الأنهار وتدعم استيطان الأسماك الحديثة في المحيط الهندي الذي حدث خلال فترة الأوليجوسين المبكرة إلى فترة الميوسين المبكرة حيث أن هذه المواقع تضم في الغالب وبشكل مثير للاهتمام أعضاء معروفين في المحيط الهندي الحالي .

الكلمات المفتاحية: الأوليجوسين، صفيحية الخياشيم الغضروفية، المحيط الهندي الهادي.

INTRODUCTION

The Oligocene is a critical long period for recording marine fishes as we face large chronological gaps in marine deposition after rapid sea level decline at the Eocene-Oligocene transition (Hansen et al. 2013; Miller et al., 2005; Zachos et al., 2001). Moreover, the dynamics of the Elasmobranchs that frequented the sub-basin of the Eastern Tethys north of the Arabian Plate are imperfectly understood during the Late Paleogene. Although there are some records of Oligocene elasmobranch assemblages in Paratethys, Western Tethys and Atlantic (e.g. Russian, Europe, North America), few are known easterly (Case and West, 1991; Adnet et al., 2007, Murray et al. 2004, 2014, Van Vliet et al., 2017) before the land bridge connection induced by the collision of the African-Arabian plate with the Eurasian plate at the late early Miocene (Harzhauser et al., 2007). The discovery of new Early Oligocene material of Elasmobranch is rather rare and an increasing knowledge on these times thus appears necessary to document the evolutionary history of fish and particularly elasmobranchs in marine oceans. There is no doubt concerning age of the Thaytiniti and Taqah Elasmobranchs because there is general agreement that the famous mammal-bearing deposits of the Ashawq Formation in the Thaytiniti area (approximatively 100km² including the formal Thaytiniti site excavated by Thomas et al. (1988, 1989) and other close localities (Al-Kindi et al., 2017) and of Taqah are Rupelian, Early Oligocene (Thomas, Roger, and Al Sulaimani, 1991a, Thomas et al. 1999, Seiffert, 2006, Seiffert et al. 2012). Indeed, these assemblages constitute original and significant amount of new elements to support the settlement of the Indian Ocean fish fauna. We can thus feature the Oman elasmobranch fauna in the Early Oligocene and discuss resemblance and differences yet existing in the sub-contemporary and geographically close locality of Paali Nala, Pakistan at this time period.

SYSTEMATICS OF ELASMOBRANCHS

Cappetta in Thomas, et al. (1989) first reported the preliminary listing of elasmobranchs from Thaytiniti collected in 1987 from excavation of 200kg of the fossiliferous deposits having delivered the teeth focused in this work. It includes *Hemipristis cf. serra ; Hemipristis aff. curvatus ; Negaprion sp. ; Galeocerdo aduncus ; Rhizoprionodon / Sphyrna ; Carcharhinus cf. amboinensis ; Nebrius sp. Chilosyllium sp. ; Rhynchobatus aff. pristinus ; Rhinobatos sp. ; Dasyastis spp. 1 et 2; Rhinoptera sp.* and *Aetobatus aff. arcuatus*. Thomas et al. (1991b) secondary analysed fossils excavated from dozens of tons of sediments from Taqah. They reported also the presence of Elasmobranch remains that consist of some shark teeth belonging to *Negaprion*, *Carcharhinus*, *Galeocerdo* and rays teeth (e.g. Dasyatidae, Rhinobatidae and Myliobatidae). Adnet et al. (2007) partially revised some of these and synonymised the *Carcharhinus cf. amboinensis* from Thaytiniti with the coeval fossil species *Carcharhinus perseus* recovered at Paali Nala (Baluchistan, Pakistan). These authors also discussed about that some *Dasyastis* from Thaytiniti preferentially belonged to *Himantura* and that the presence of a weak serrated mesial cutting edge suggests a transitional form between *H. curvatus* and *H. serra* justifying the attribution in confer to *H. serra* rather than *H. serra*. Restudying the material collected during the original fieldtrip in 1987, we perform the updating listing with figurations of elasmobranches from Thaytiniti that now consist of: *Hemipristis cf. serra (rare) ; ?Moerigaleus sp. (rare), Negaprion sp. (frequent); Galeocerdo aduncus (rare) ; Rhizoprionodon (common); Carcharhinus perseus (common); Nebrius sp. (rare); ?Stegostoma sp. (rare); Chilosyllium sp. (common) ; Rhynchobatus aff. pristinus* (*common*) *; "Rhinobatos" sp. (common) ; Himantura sp. (frequent); ?Taeniura sp. (common), Dasyatid indet (rare) Rhinoptera sp. (rare); Aetobatus aff. arcuatus (rare).* It appears that Taqah fauna is quite similar with occurrence of dominance of *Himantura sp. and ?Taeniura sp.* and unsignalled presence of *Rhynchobatus aff. pristinus*

All the Elasmobranch specimens from historical Thaytiniti locality recovered in 1987 fieldtrips and presently figured in this work are now housed at the Department of Archaeology, Ministry of Heritage and Tourism of the Sultanate of Oman (reference DA plus catalogue number) from DA53445 to DA53457.

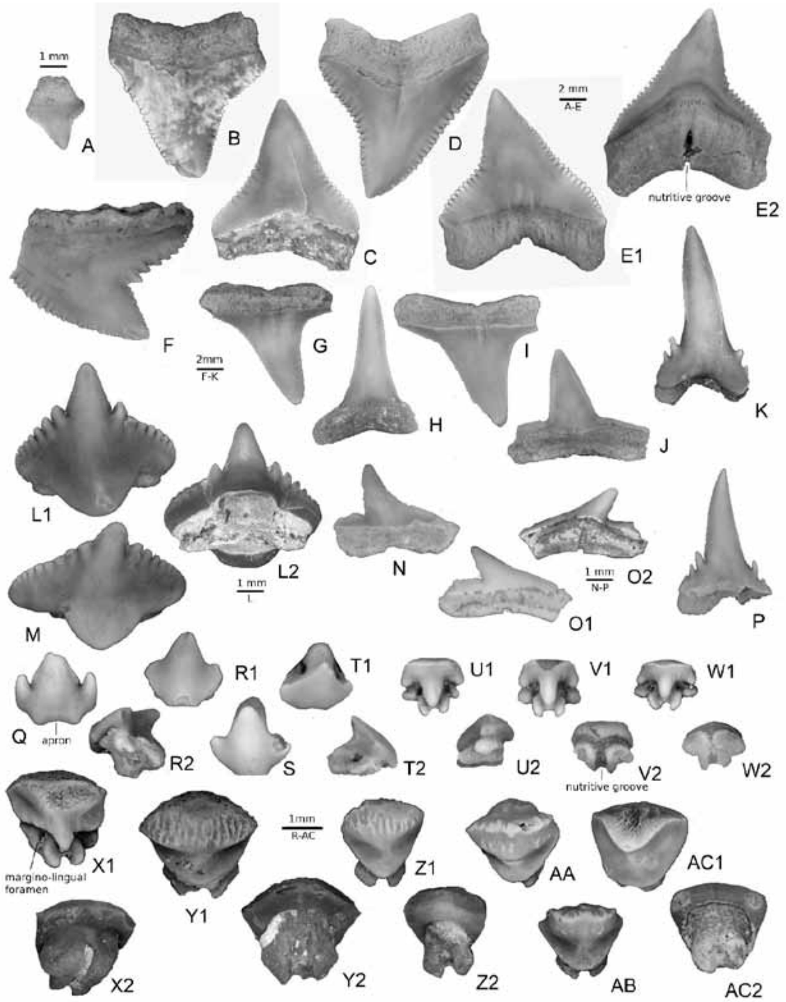

Figure 1: *Thaytiniti elasmobranch teeth recovered in 1987. A-E Carcharhinus perseus: A(DA53445/1) symphyseal upper tooth (labial view), B(DA53445/2) anterior upper tooth (labial view), C(DA53445/3) antero-lateral upper tooth (labial view), D(DA53445/4) lateral upper tooth (labial view), E(DA53445/5) lateral upper tooth, E1(labial view), E2(lingual view); F. Galeocerdo aduncus (DA53446): lateral tooth (labial view) ; G-J. Carcharhinus sp or Negaprion sp.: G (DA53447/1) antero-lateral upper tooth, H (DA53447/2) lower anterior tooth, I (DA53447/3) antero-lateral upper tooth, J DA53447/4) lateral lower tooth (labial views); K. Hemipristis cf. serra (DA53448) anterior upper tooth (labial view); L-M Nebrius sp.: L (DA53449/1) anterior tooth L1(labial view), L2 (lingual view), M (DA53449/2) lateral tooth (labial view); N-O. Rhizoprionodon sp.: N (DA53450/1) anterior tooth, O(DA53450/2) lateral tooth (labial views); P. ?Moerigaleus sp. (DA53451) lower anterior tooth (labial view); Q. ?Stegostoma sp. (DA53452) anterior tooth (labial view); R-T. Chiloscyllium sp : R(DA53453/1) anterior tooth R1(labial view), R2(semi profile), S(DA53453/2) anterior tooth (occlusal view), T(DA53453/3) lateral tooth T1(occlusal view),T2(profile) , U-W. Rhinobatos sp. :U(DA53454/1) anterior tooth U1(lingual view), U2(profile), V(DA53454/2) antero-lateral tooth V1 (lingual view),V2(labial view),W(DA53454/3) lateral tooth W1(lingual view),W2(basal view); X. Rhynchobatus cf. pristinus (DA53454) lateral tooth X1(lingual view), X2(oblique labial view); Y-Z. Himantura sp. : Y(DA53455/1) lateral tooth Y1(lingual view),Y2(labial view), Z(DA53455/2) anterior tooth Z1(lingual view), Z2(labial view); AA-AB. . ?Taeniura sp. : AA (DA53456/1), anterior tooth (oblique occlusal view), AB(DA53456/2), anterior tooth (lingual view) ; AC. Dasyatidae sp (DA53457), anterior tooth AC1 (lingual view), AC2 (basal view)*

ORECTOLOBIFORMS

Ginglymostomatidae Gill, 1862

Nebrius sp. (Figure 1L-M)

Figured material: anterior tooth (DA53449/1), lateral tooth (DA53449/2).

Description and Discussion: The anterior tooth crown (Figure 1L) has a high median cusp flanked by numerous mesial and distal cusplets that decrease in size towards the crown margins. The more lateral tooth (Figure 1M) has more cusplets on mesial side of cusp than on distal side, resulting in strong crown asymmetry. Prominent labial apron is present in anterior and lateral teeth, which is not bifid and uniformly rounded. Lingual crown face is smooth (Figure 1L2) and roots are unfortunately missing in both teeth. Anterior tooth morphology (Figure 1L) is quite different from those often referred in Eocene deposits (e.g. *Nebrius obliquus* (Leidy, 1877), *Nebrius thielensis* (Winkler, 1874) and *Nebrius blanckenhorni* (Stromer, 1903)) in having a higher, erected median principal cusp. *N. obliquus*, *N. thielensis* and *N. blanckenhorni* are very common carpet sharks recovered in the Eocene warm to tropical nearshores deposits worlwide (Underwood et al., 2011; Cappetta, 2012; Cappetta and Case, 2016; Ebersole, Cicimurri, and Stringer, 2019; Adnet et al., 2020; Samonds et al., 2019). Numerous observations based on more abundant material (Noubhani and Cappetta, 1997; Cappetta and Case, 2016; Ebersole, Cicimurri, and Stringer, 2019) often doubted about systematics validity of these three coeval Eocene species. Post Eocene reports of *Nebrius* are strangely scarcer, particularly during Oligocene period. They only concern those from Chattian of South Carolina (referred as *N. cf. serra*. Cicimurri and Knight 2009), of North Carolina (Müller 1999 according Cicimurri and Knight 2009) and some from Rupelian of France (Génault, 1993). Yabumoto and Uyeno (1994) and Cicimurri and Knight (2009) assigned some fossil *Ginglymostoma* teeth with numerous lateral cusplets (e.g. *G. delfortriei*, *G. serra*) to *Nebrius* even if other (Cappetta, 2012) consider that *Nebrius* teeth are first characterized by a moderately high and thick, distinctly asymmetrical crown with an extremely developed apron passing beyond the basal plane of the root in mesial view, where apron in *Ginglymostoma* is shorter and sometimes bifid. Whatever the future of systematics debate, the Thaytiniti specimens are morphologically similar to those attributed to *Nebrius* cf. *serra* (Leidy, 1877) from Late Oligocene of USA (Cicimurri and Knight, 2009) as those from the late Middle Eocene of Tunisia (Adnet et al, 2020) reported as *Nebrius* sp. Rarity and fragmentary state of preservation of teeth does not allow a better attribution.

Stegostomatidae Gill, 1862

Cf. *Stegostoma* sp. (Figure 1Q)

Figured material: anterior tooth (DA53452).

Description and Discussion: A unique fragmentary anterior tooth (figure 1Q) could be attributed to zebra shark *Stegostoma.* The crown is quite symmetrical and bears a broken main cusp which is flanked by a pair of lateral cusplets. The latter are strong, erected and well-individualized from the cusp. Both lateral cusplets are similarly sharply pointed and all of the cusps possess sharp cutting edges. Beneath the central cusp base, one can observe a moderate bifid apron on the crown margin as observable in living *S. fasciatum* (Herman, Hovestadt, and Hovestadt, 1992). Tooth partially resemble to the Middle-Late Eocene *Stegostoma tethysiensis* Adnet et al., 2020 but lateral cusplets seem lesser developed unless broken tooth belong to a lateral file.

Hemiscyllidae Gill, 1862

Chiloscyllium sp. (Figure 1R-T)

Figured material: anterior tooth (DA53453/1), anterior tooth (DA53453/2), and lateral tooth (DA53453/3).

Description and Discussion: The rare teeth are small (less than 2 mm in length) and show a principal and symmetric cusp, large apron and a pair of well-developed shoulders often making minute hook-like denticles. With teeth symmetrical, possessing a convex labial face of crown, a straight cusp with small lateral shaped cusplets, these teeth belong preferentially to *Chiloscyllium* rather than to *Hemiscyllium* according to Herman & Crochard (1977) and Herman, Hovestadt, and Hovestadt (1992). Until now; there were no post Eocene report of these Indo-Pacific bamboo sharks (Hemiscyllids, *Chiloscyllium*) if we exclude the dubious damaged crown of cf. *Chiloscyllium* from Neogene of Brazil (Aguilera et al., 2017). Teeth of this undescribed species clearly reminds that of living species (e.g. *Chiloscyllium punctatum* or *Chiloscyllium griseus*) and is probably conspecific with that recorded in Paali Nala (Pakistan) as Orectolobiformes indet. by Adnet et al. (2007).

CARCHARHINIFORMS

Carcharhinidae Jordan and Evermann, 1896

Carcharhinus perseus Adnet et al., 2007 (Figure 1A-E)

Figured material: symphyseal upper tooth (DA53445/1), anterior upper tooth (DA53445/2), antero-lateral upper tooth (DA53445/3), lateral upper tooth (DA53445/4), and lateral upper tooth (DA53445/5).

Description and Discussion: Specimens from Thaytiniti display size and morphological features very similar to those observable in the species *C. perseus* (Adnet et al., 2007), with a very limited dignathic heterodonty, a reduced nutritive groove (in lingual view Figure 1E2) and a strong labio-lingual compression of teeth. *C. perseus* was originally described from the Rupelian of Paali Nala, Baluchistan, Pakistan (Adnet et al., 2007) and is also known from the Rupelian of Egypt (Jebel Qatrani, Quarries A and E; Murray et al., 2014; Qattara Depression: Van Vliet et al., 2017) and from the Eocene/Oligocene boundary of Tunisia (Sweydan et al. 2019). Previously signalled as present in Thaytiniti (Adnet et al., 2007: in text), Figures 1A-E definitively testify occurrence of the Pakistani species. All these reports testify that the tropical *Carcharhinus perseus* is clearly distinguishable and extremely modern compared to contemporaneous species of *Carcharhinus* from higher latitude localities (*C. elongatus* or *C. gibessi*). The last ones having upper teeth with mainly erected central cusp with smoothed cutting edge and slightly to heavy serrated shoulders (Reinecke, Stapf, and Raisch, 2001; Reinecke et al., 2005; Feichtinger et al., 2019).

?Negaprion sp. or ? *Carcharhinus* sp. (Figure 1G-J)

Figured material: antero-lateral upper tooth (DA53447/1), lower anterior tooth (DA53447/2), antero-lateral upper tooth (DA53447/3), and lateral lower tooth (DA53447/4).

Description and Discussion: This taxa is represented by several specimen that seem to exhibit strong dignathic heterodonty, with antero-lateral upper teeth (Figure 1G,I) having a broader cusp flanked by elongate, oblique lateral shoulders (sometimes notched) whereas lower lateral teeth (Figure 1H, J) have a erected, narrower cusp and smooth shoulders that are nearly perpendicular to the cusp in lateral files (Figure 1J). We are not sure if all specimens belongs to the same taxa or represents a composite set from several carcharhinid. Considering that material comes from a unique taxa, it remains those of *Negaprion* rather than *Carcharhinus* (e.g. shoulders sometimes slightly notched on upper teeth, no serration on both jaws and lower anterior teeth with relatively long cusp compared to root). However confusions between fossil teeth of *Negaprion* and those belonging to fossil *Carcharhinus* with smoothed cutting edges are notable and relatively usual concerning the Eocene- Early Oligocene specimens (Sweydan et al., 2019) leading some authors to undifferentiate the occurrences of *Carcharhinus* from those of *Negaprion* (e.g. Kriwet, 2005; Underwood and Gunter, 2012 ; Sweydan et al., 2019). Morphology of Thaytiniti specimen seem however different from those of the Late Eocene ?*Carcharhinus frequens* (Dames, 1883) observed in Rupelian deposits of the Qattara Depression (as *Negaprion*, Van Vliet et al., 2017) and of the Fayum (Quarries R and E, as *Carcharhinus* sp. in Murray et al., 2014: Figure 4) in Egypt. They also differ from Late Eocene *?Negaprion* or *?Carcharhinus* sp. recovered until the Latest Eocene-Earliest Oligocene of Tunisia (Sweydan et al., 2019) and from the greater *Negaprion* sp. from Rupelian of Pakistan (Adnet et al., 2007).

Rhizorpionodon sp. (Figure 1N-O)

Figured material: anterior tooth (DA53450/1), and lateral tooth (DA53450/2).

Description and Discussion: Post Eocene evidences of *Rhizoprionodon* are relatively common in tropical worldwide deposits leading some authors to propose that the current distribution of the seven recent species is most likely a result of a former widespread distribution along Tethyan mangroves in the mid-Cenozoic, affected by successive vicariance events (Briggs, 1995; Musik et al., 2004; Gallo et al., 2010). Besides the fact that tooth morphology of fossil *Rhizoprionodon* is quite conservative, dignatic and gynandric heterodonties are frequently observed in fresh jaws of Recent representatives (Adnet et al., 2020) leading its use in systematics from a poor sample highly uncertain.

Galeocerdonidae Poey, 1875

Galeocerdo cf. aduncus Agassiz, 1843 (Figure 1F)

Figured material: lateral tooth (DA53446).

Description and Discussion: Morphologically closed to the living species, teeth of *G. aduncus* are often separated from extend species *G. cuvier* based on the size as well as the absence of secondary serrations on the mesial cutting edge (Applegate 1978; Cigala-Fulgosi and Mori 1979; Kent 2018). They are however sometimes confused or synonymised with this later, considering they belong to its juveniles (Purdy et al., 2001). Türtscher et al., (2021) recently confirmed the systematics statute for this common fossil species known worldwide from Early Oligocene to Late Miocene and previously recorded in the Early Miocene of Sharbithat (Adnet and Charpentier, 2022).

Hemigaleidae Hasse, 1878

?*Moerigaleus* sp. (Figure 1P)

Figured material: lower anterior tooth (DA53451).

Description and Discussion: The crown is either unornamented. Tooth is strongly compressed labiolingually and the cusp is high compared with the root. The unique upper anterolateral tooth (Figure 1P) bears a pair a pair of minute hook-shaped denticles below its both cutting edges. The rare material available here reminds those of the unique species *M. vitreodon* from the Late Eocene of Egypt, a fossil hemigaleid shark known since the Lutetian-Bartonian period (Underwood and Ward, 2011; Adnet et al. , 2020). Its occurrence until Early Oligocene must be now confirmed. Cappetta in Thomas et al. (1989) probably confused this with Eocene species *Hemipristis curvatus.*

Hemipristis cf. *serra* Agassiz, 1843 (Figure 1K)

Figured material: anterior upper tooth (DA53448).

Description and Discussion: Fragment of upper teeth and one sub complete anterior lower tooth (Figure 1K) could confirm presence of this worldwide great shark reported since the Early Oligocene (e.g., Adnet et al., 2007; Van Vliet et al., 2017) until the Pleistocene of Alabama (Ebersole, Ebersole, and Cicimurri, 2017). The lower anterior tooth (Figure 1K) has unserrated, long, pointing and lingually inclined cusp with two pair of minute cusplets near the base. The cutting edges, salient, do not reach the base of crown. Root is bilobed with crown extinctions well overlaying the root lobes in labial view. Succeeding to the Eocene *Hemipristis curvatus*, the lower teeth of *H. serra* easily distinct from its supposed ancestor by having elongated sigmoid cusp with basally interrupted cutting edges and flanked by one to several pairs of hooked secondary denticles as figurate in the Early Miocene of Sharbithat (Adnet and Charpentier, 2022: Fig. 3 IJ).

RHINOPRISTIFORMS

Rhinobatidae Bonaparte, 1835

“Rhinobatos” sp. (Figure 1U-W)

Figured material: anterior tooth (DA53454/1), antero-lateral tooth (DA53454/2), lateral tooth (DA53454/3).

Description and Discussion: Relatively common in the Cretaceous-Paleogene levels, oral teeth of this genus are often confused with those of Pristids before Middle Eocene and appearance of the characteristic rostral denticles of the last ones (Cappetta, 2012). No partial or complete rostral denticle of Pristid was found in material recovered at Thaytiniti nor at Taqah. Fossils of guitarfish, with its forty living species around the world, are surprisingly scarce in Oligocene (Adnet et al. 2007) and also in Neogene assemblages (e.g. Cappetta, 1970; Sahni and Mehrotra, 1981; Antunes, Balbino, and Cappetta, 1999; Reinecke et al., 2011; Sharma and Patnaik, 2013). Oman species (and the coeval specimen from Pakistan) differ from European Miocene species *R. antunesi* (Jonet, 1968) in having a more gracile shape, a lower crown with more developed pair of lateral uvulae and a larger and better marked nutritive groove on basal face of root. The unique lateral tooth of *R. sahnii* Sahni and Mehrotra, 1981 from the Lower Miocene of India could resembles our material, however the lingual extension of root lobes in *R. sahnii* seems lesser developed. Most of the fossil teeth attributed to *Rhinobatos* (Cappetta, 2006) are probably confused with that of guitarfish genera recently rehabilitated in systematics (e.g. *Glaugostegus, Platyrhinoides, Aptychotrema, Pseudobatos, Acrotheriobatus, Trygonorrhina*) but their precise dental morphologies are mainly unknown except for three species (Herman et al 1997; Cappetta 2012). We note that root of *Rhinobatos* sp from Thaytiniti preferentially resemble to that of *Glaugostegus cemiculus* (Herman et al. 1997). Only a deep study of Recent species would probably allow to correctly define tooth characters of the guitarfish taxa.

Rhinidae Müller & Henle, 1841

Rhynchobatus aff. *pristinus* (Probst, 1877) (Figure 1X)

Figured material: lateral tooth (DA53454).

Description and Discussion: The teeth have a massive appearance, symmetric to slightly asymmetric in lateral files (Figure 1X). The oral face of the crown may be differentiated into a labial area, more or less convex and an occlusal area that has a triangular shape separated from the previous one by a clear straight crest. Both presenting ornamentation of enameloid granules (Figure 1X1). A third area, the lingual area smooth and bears a well-developed enameled protuberance forming a long central uvula. The root is massive with two lobes well separated by a deep groove. On the lingual face of the root, and on each side of the uvula, there is a well-marked depression with a big margino-lingual foramen. The teeth of *R. pristinus* are commonly reported in all the Oligo-Miocene deposits around the world (e.g. Cappetta 1970, 2012) and it is likely that they belong in fact to several species.

MYLIOBATIFORMS

Dasyatidae Jordan & Gilbert, 1879

Himantura sp. (Figure 1Y-Z)

Figured material: lateral tooth (DA53455/1), and anterior tooth (DA53455/2).

Description and Discussion: Teeth are medium sized reaching 4mm length. The lack of well-detached cusp, the presence of an enameloid ornamentation over the occlusal part of the lingual face and over the entire labial face of crown, the presence of a short root with well-detached root lobes where an unique labial foramen opens remind the dental condition observable in many urogymnin like *Himantura*, *Pateobatis* or *Maculabatis.* Few fossils are clearly associated to these genera due to the volatility of synonymy among the dasyatids (Last, Naylor, and Manjaji-Matsumoto, 2016). Most of fossils of *Dasyatis* recovered by teeth need to be revised but the lack of illustrations of teeth of such extant taxa remains unknown for paleontologists (Guinot et al., 2018). These teeth however remain that is observable in *H. souarfortuna* from the mid Eocene of Tunisia (Adnet et al., 2020), in Miocene *Himantura menoni* or *Himantura* spp. from of Peninsular India (Shani and Merohtra, 1981; Sharma and Patnaik, 2013; Sharma et al., 2022*),* Madagascar (Andrianavalona et al., 2015) and Brunei Darussalam (Kocsis et al., 2018) respectively. Restudy of Early Oligocene Pakistan material from Paali Nala (Adnet et al. 2007) suggest that Oman and Pakistan species, even unnamed, are clearly conspecific. Today the modern species of this whipray live in the Indo-Pacific region. They inhabit inshore waters but some have also been reported from lagoons, brackish estuaries and mangrove swamps (Last, Naylor, and Manjaji-Matsumoto, 2016)

?*Taeniura* (Figure 1AA-AB)

Figured material: anterior tooth (DA53456/1), and anterior tooth (DA53456/2).

Description and Discussion: Teeth are smaller sized compared to previous dasyatid (Figure 1Y-Z). Crown is relatively high and its occlusal part (mainly formed by transversal crest) is irregularly domed. Lingual face of crown is triangular shaped and enameloid is mainly smooth. At the contrary, enameloid of the labial face of crown has a few irregular ridges. Without deeply ornamented enameloid on labial face, the tooth morphology is quite different from Neogene *Taeniurops cavernosus* (Probst, 1877), *Dasyatis rugosa* and *Dasyatis delfortiei* Cappetta, 1970 also sometimes reported in Oligocene deposits. On the other hand, teeth remind that tooth from Early Oligocene of Egypt figured as *Taeniura* sp. (Murray et al., 2014). Unfortunately, no study of tooth morphologies within the most diversified subfamilies of Dasyatid (Dasyatinae, Neotrygoninae and Urogymininae) is available due to incompleteness of tooth figuration (Guinot et al., 2018), justifying we reserve our generic attribution.

Dasyatidae indet (Figure 1AC)

Figured material: anterior tooth (DA53457).

Description and Discussion: Crown morphology of some teeth is quite singular for a dasyatid and does not correspond to both previous species. Transversal crest is well-developed, sharped and form a pseudo cusp, flat and few elongated medio-lingually. Lingual face of crown is as large as high, entire smooth and largely overlap the root lingually. Labial face of crown is relatively flat to concave and is covered with a very finely serrated enameloid. Root is narrow and root lobes, often damaged, seem few extended lingually. At the present time, these fossil remains available (teeth) did not allow recognition a given Dasyatid-like genus.

Rhinopteridae Jordan & Evermann, 1896

Rhinoptera sp. (not figured)

Description and Discussion: Among other characters, teeth of *Rhinoptera* differ from those of *Myliobatis* in the absence of a distinct shelf at the crown base and in having more regular hexagonal outline in occlusal view. Unfortunately, no complete teeth are conserved forcing us to reserve our determination.

Myliobatidae Bonaparte, 1835

Aetobatus sp. (not figured)

Description and Discussion: Unfortunately, the dental plate of this malacophageous ray is only recorded by some fragmentary teeth. The identified fragments are principally those of the upper teeth. The teeth are fairly rectilinear except the lateral edges which are curved towards the back. The width of the crown decreases toward the lateral extremities as in any *Aetobatus*. The external face of the teeth is sub-vertical while the internal face is oblique. The root bends lingually and is composed of a succession of grooves and laminae. Isolated teeth of this genus are commonly reported in Cenozoic deposits but only complete dental plates allow serious identification (Hovestadt. and Hovestadt-Euler, 2013).

DISCUSSION

PALEOENVIRONMENT OF EARLY OLIGOCENE MARINE DEPOSITS

The environment at Thaytiniti was first considered as shallow coastal marine (Thomas et al., 1989) due to the mix of marine species (e.g. elasmobranches) and terrestrial gastropod, reptiles and mammals (Thomas et al., 1988, 1989, 1999; Thomas, Roger, and Al Sulaimani, 1991a; Pickford et al. 1994, 2014, Pickford 2015). Otero and Gayet (2001) secondary studied the bony fish fauna of Thaytiniti. This last was mainly composed of stenohaline freshwater fishes (teleosts and the dipnoan Protopterus) living in different freshwater environments on the continent (swamps and running waters), of freshwater taxa that tolerate temporarily marine sea in estuaries (e.g. some teleosts and a crocodilian Gavialidae) and marine fish including diodontids (porcupine fish) and elasmobranchs. These last authors concluded that the presence of a mixed marine and freshwater ichthyofaunas (probably transported to the seashore as the floating mammals carcass), preserved as separated elements only, agrees with first paleoenvironmental interpretation. Later, Adnet et al. (2007) suggested also that the contemporaneous Paali Nala sands from Baluchistan (Pakistan), recording a very close elasmobranch associations of Thaytiniti, were probably deposited in a brackish zone of a large river near an estuary. The modern elasmobranch association from Thaytiniti (dominated by carcharhinids in frequencies and diversity) makes it directly comparable with those of the tropical recent coasts (Compagno, 1990). Abundance of carcharhinids, stingrays and guitar rays are all indicative of an extreme littoral habitat in tropical latitude; pelagic usual Oligocene elasmobranchs frequenting more open seas (e.g. Lamniformes) being entirely absent of both localities. In addition, all the living sharks and rays usually considered as representatives to the Thaytiniti (and also Taqah) fossils are mostly euryhaline species known to occur on or adjacent to continental and insular shelves, frequenting river estuaries (*e.g. Galeocerdo cuvier, Nebrius spp, Chiloscyllium spp, Rhizoprionodon spp., Rhynchobatus spp.*) and/or penetrate tropical rivers (*e.g., Carcharhinus leucas or C. amboinensis, Negaprion acutidens and Rhinobatos species) as well as to live exclusively in freshwater (some species of Dasyatis/Himantura*). In agreement with the previous fossil studies from Thaytiniti, the presence of a mixed coastal marine, brackish to freshwater elasmobranchs agrees with previous paleoenvironmental interpretations (Figure 2).

The environment at Taqah was more precisely reconstructed (Thomas et al., 1991b; Roger et al., 1993) from a multidisciplinary study based on excavation and screening of several tons of sediments. All the fossils, including also many terrestrial mammals (Sigé et al., 1994) and sedimentological evidences from fossil-bearing level of Taqah seem indicate that this horizon accumulated in a shallow costal swamp, sporadically influenced by sea, under hot and semi-arid climate. Elasmobranch fauna from Taqah seems drastically lower diversified compared to those from Thaytiniti, suggesting a more confined marine area than in Thaytiniti.

Figure 2: *Possible reconstitution of Thaytiniti locality at Early Oligocene. Asteroida and Decapod Xanthidae/ Calappidae (Thomas et al. 1989) ; Tetraodontidae (Otero & Gayet, 2001) ; Rhinid; Carcharhinid (e.g. Carcharhinus perseus) and Dasyatid (e.g. Himantura) (this work).*

OLIGO-MIOCENE ELASMOBRANCHS, THE RISE OF MODERN TROPICAL LIFE

This work is first a new contribution to the paleontological studies devoted to fossil remains of Elasmobranchs in the Sultanate of Oman that are currently limited to teeth, dermic denticules and fin spines of Ctenacantiforms and Hybodontiforms from Haushi-Hugf , Mountains at Jabal Safra, Wadi Alwa and Wadi Wasit, Middle Permian–Lower Triassic (Koot et al. 2013, 2015) ; a spine remain of ray from the Hugf region (Roger et al. 1994) and teeth from Sharbithat region (Charpentier, Adnet, and Cappetta, 2020; Adnet and Charpentier, 2022), Early Miocene (Figure 3). The Early Oligocene tropical seas were clearly different geographically from today, especially around the Middle East. The Proto Mediterranean Sea (namely Western Tethys also ramified north-easterly to the Paratethys, a gigantic interior sea) and the Indian Ocean are still connected by Eastern Tethys north of the Arabian Plate (Meulenkamp and Sissingh 2003). For long the only Oligocene Indian Ocean Elasmobranch elements were known through the fossil locality of Paali Nala, Pakistan (Adnet et al., 2007) if we exclude the frequent reports of the preliminary listing from Thaytiniti available in Thomas et al. (1989).

Other contemporaneous Elasmobranch fauna from Eastern Tethys are only represented by the Rupelian associations from Minqar Tibaghbagh, Egypt (Van Bliet et al., 2017 with *Hemipristis cf. serra, Carcharhinus cf. perseus, carcharhinus sp., Negaprion frequens, Galeocerdo sp., Carcharias, sp., Otodus (Carcharocles) cf. sokolowi and “Aetobatus” sp.*) and those from the Jebel Qatrani Formation of the Fayum Depression, Egypt too (Murray, 2004; Murray et al. 2014 with *Carcharhinus cf. C. perseus, Carcharhinus sp., Aetobatus sp., Galeocerdo sp., cf. Misrichthys stromeri; Rhinoptera sp. , Pastinachus sp. Dasyatis sp., Odontorhytis sp.*).

All the taxa recovered at Thaytiniti and Taqah, except *Moerigaleus, ?Stegostoma*, are known at Paali Nala (Adnet et al. 2007) and belong to modern genera that currently frequent the Indo Pacific oceanic realm. Their presence in Early Oligocene deposits of Oman coast was thus predictable and the formal reporting of fossil bamboo shark, zebra shark and guitarfish recovered here ascertain the oldest record of modern representatives in the fossil Indian Ocean. Large oceanic sharks recovered in locality of the Egyptian Western Desert (e.g. *Otodus (Carcharocles) cf. sokolowi; Carcharias,* sp.) are unknown at Thaytiniti and Taqah and these lacks from their fossil-bearing levels are relative to the shallow costal swamp condition of deposits, as also observed in Paali Nala.

Oligocene Elasmobranch records are relatively scarce compared to other periods, often reduced to isolated taxa, they principally come from highest latitudes of Paratethys (Bienkowska-Wasiluk and Radwanski 2009; Szabó and Kocsis, 2016; Cappetta, Gregorova, and Adnet, 2016, Szabó et al., 2017, Prokofiev and Sychevskaya, 2018) ; North Atlantic (Bor, 1990; Hovestadt and Hovestadt-Euler, 1999, 2002 Cicimuri and Knight 2009, Shimada, Welton, and Long, 2014; Mollen 2007; Mollen, Van Bakel, and Jagt, 2016; Reinecke, Stapf, and Raisch, 2001; Reinecke et al, 2014, Reinecke, Von der Hocht, and Dufraing, 2015; Reinecke et al., 2020) and North Pacific (Applegate and Uyeno, 1965, Uyeno, Yabumoto, and Kuga, 1984,Tomita and Oji, 2010, Welton, 2016ab; Welton and Goedert, 2016).

If many worldwide Early Oligocene taxa are commonly observed in Oman (e.g. *Hemipristis, Negaprion, Carcharhinus, Galeocerdo, Nebrius*), none of these high-latitude localities have recovered the modern Eastern Tethysian taxa *Carcharhinus perseus,* cf. *Stegostoma, Chilloscylium* nor “*Rhinobatos”*. Moreover, diversity in lamniforms is significantly greater in highest latitudes deposits than in Eastern Tethys where carcharhiniforms already domine assemblages. The presence of modern taxa belonging to eleven families including many Carcharhiniforms and Orectolobiforms (large requiem shark, zebra and bamboo shark, stingray, guitarfish) in Egypt, Oman and Pakistan stresses in the Eastern Tethysian ichthyofauna the Indo Pacific stamp ever noticed for Late Paleogene deposits. Initiation of polar ice sheets with the Antarctic glaciation near the end of the Eocene has been closely linked to the global cooling of the Eocene/Oligocene boundary. Fall to 26°C during Earliest Rupelian (~33My), the tropical sea surface temperature quickly returned to warmer conditions (30°C ~29My) according O'Brien et al. (2020). The tropical Rupelian Elasmobranch fauna recovered in Oman, Pakistan and Egypt do not testify of any faunal change that could be indicative of temperature fall recorded in Earliest Rupelian.

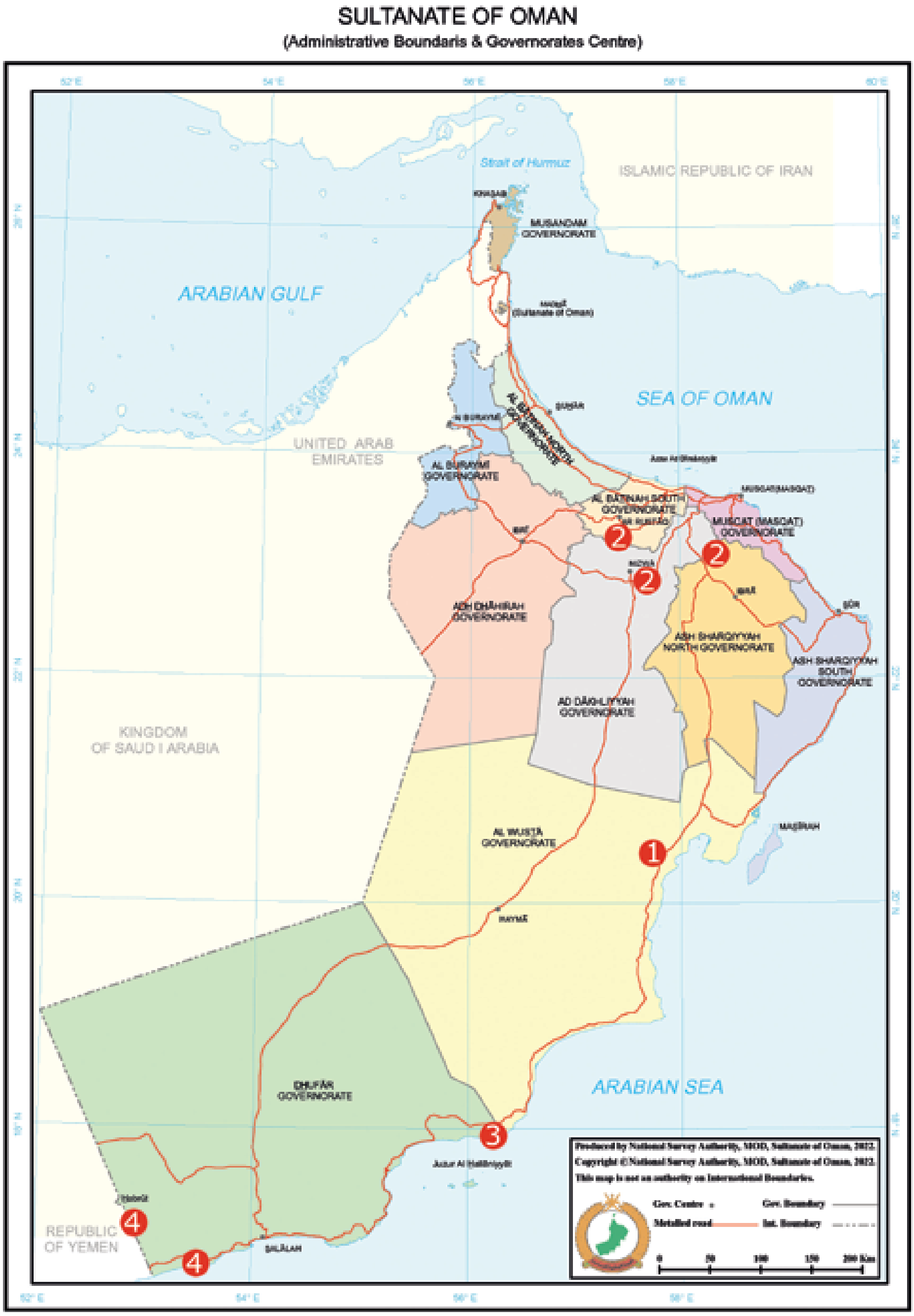

Figure 3: *Oman localities with fossil elasmobranchs: 1. Middle Permian from Haushi-Huqf area (Roger et al., 1994 ; Koot et al., 2013), 2. Permo-Triassic from the Oman Mountains at Jabal Safra, Wadi Alwa and Wadi Wasit (Koot et al., 2015); 3. Early Miocene from Sharbithat area (Charpentier, Adnet, and Cappetta, 2020; Adnet and Charpentier, 2022); 4. Early Oligocene from Thaytiniti and Taqah areas (Thomas et al., 1989, this work).*

The future description of a much richer assemblages from those localities is possible due to the combination of a new wave of field project including the systematic use of screening sampling methods on fields. Like ever evidenced in younger site recovered in Oman (Charpentier, Adnet, and Cappetta, 2020; Adnet and Charpentier, 2022) and elsewhere around Indian Ocean (Priem 1907; Mehrotra et al., 1973 ; Sahni & Mehrotra, 1981 ; Andrianavalona et al., 2015; Sharma et al., 2022), an important part of the Elasmobranch diversity might be easily revealed by their teeth. This is particularly interesting with fossiliferous marine deposits before the mid-Miocene closure of Eastern Tethys induced by the collision of the African–Arabian plate with the Eurasian plate to precisely track what is considered to be a major driver of tropical marine biodiversity (Cowman and Bellwood 2013; Harzhauser et al. 2007; Renema et al. 2008; Malaquias and Reid 2009; Hou and Li 2018; Liu et al. 2018).

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* In Memoriam of Henri Cappetta, passed away before the final publishing of this article*.

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